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TREMPEALEAUIAN TRILOBITES FROM THE CONOCOCHEAGUE, FREDERICK, AND GROVE LIMESTONES OF THE CENTRAL APPALACHIANS

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ABSTRACT—The Conococheague formation of the Cumberland-Shenandoah valleys of Pennsylvania, Maryland, and Virginia was known to represent most of the Croixian series, but only a few Franconian and 2 Trempealeauian fossils had been published. A faunule of Trempealeauian age including 15 species is described from the upper Conococheague of Pennsylvania and Maryland. The Frederick limestone of Maryland yielded 19 species of Trempealeauian trilobites, of which only one was previously known from the formation. The overlying Grove limestone, hitherto considered entirely Lower Ordovician on the basis of brachiopods and cephalopods collected in the upper part of the formation, yielded a faunule of 11 Trempealeauian trilobites near the base, indicating that the Cambrian-Ordovician boundary lies within the formation. All these faunules have many genera and species in common with the *Hungaia magnifica* boulders at Levis, Quebec, the Gorge formation of northwestern Vermont, and the Eminence dolomite of the Ozark uplift.

One new genus, *Conococheaguea* (type species: *C. ovata*, n. sp.) and the following new species are described: *Apatokephaloides macrops*, *A. minor*, *Aposolenopleura plicata*, *Bowmania pennsylvanica*, *Keithia intermedia*, *Idiomesus intermedius*, *Levisella nasuta*, *Prosaukia corrugata*, *Richardsonella subcristata*, and *Triarthropsi limbata*.

INTRODUCTION

THE Conococheague limestone of the Cumberland-Shenandoah valley of Pennsylvania, Maryland and Virginia and the Frederick and Grove limestones of the Frederick valley of Maryland have been searched for fossils by many geologists and paleontologists with meager results. The Conococheague formation yielded trilobites from various horizons at scattered localities, indicating that its deposition spanned most of the Late Cambrian and a portion of the Canadian epochs. Fossils were even much scarcer in the Frederick limestone, the known forms indicating a Trempealeauian age. The Grove limestone yielded several species of brachiopods and cephalopods definitely identified as Early Ordovician.

The author's collections from the Trempealeauian strata of these formations have produced fossils in considerably greater numbers and better state of preservation than those previously available. It is deemed worth while to describe these faunules to establish a more precise correlation with formations in other areas, and in some cases also for the contribution to the morphology and distribution of trilobite genera and species. The relatively large Dresbachian and Franconian faunules will be described in another paper.

All the significant fossils recovered are

trilobites. In addition, only poorly preserved gastropods and brachiopods were observed, whose description would bring no appreciable contribution either to paleontology or biostratigraphy. All the specimens figured herein were collected by the writer, excepting one specimen of *Plethometopus obtusus* collected by Dr. James L. Wilson, one of *Euptychaspis typicalis* collected by Dr. William J. Sando, and one free cheek of "*Acidaspis*" *ulrichi* from the U. S. National Museum collections. The author is indebted to Dr. Wilson and Dr. Sando for the loan of their collections. All the types of new species and other figured specimens were deposited in the U. S. National Museum collections. The author is greatly indebted to the Geological Society of America for a project grant.

STRATIGRAPHY AND FAUNAS

Conococheague formation.—Scattered occurrences of Trempealeauian fossils in the upper Conococheague were known from several localities in Pennsylvania, Maryland and Virginia (Wilson 1951, 1952; Sando, 1957). Two trilobites, *Saukia stosei* Walcott and *Tellerina scotlandensis* Resser, had been previously described, both from the vicinity of Chambersburg, Pennsylvania. Examination of the known localities and numerous other exposures yielded a faunule sufficiently characteristic and well preserved to warrant description only at two localities. One is Wilson's locality 47-9w, northeast of Chambersburg. Unfortunately, only a small portion of the section can be studied here, hence the position of the fossiliferous beds with respect to the base or top of the formation cannot be determined. Most of the strata are exposed in a shallow, abandoned quarry where the dip is 20°W 30°S (however, strike and dip vary quite irregularly in this area). The quarry exposes 12–15 feet of partly aphanitic, partly crystalline or oölitic, thick-bedded, dark-gray limestone, underlain and overlain by the more typical, thin-bedded Conococheague limestone. Possibly the thick-bedded limestone is a local lens. Fossils were collected in a limestone nodule interstratified with siliceous layers 37 feet above the top of the thick-bedded limestone (locality cca/1). Here the only species present is *Prosaukia corrugata* Rasetti n.sp. All the other trilobites were recovered in the quarry (loc. cca) from 8 to 10 feet above the base of the thick-bedded limestone, where fossils are relatively common. The faunule includes:

Bowmania pennsylvanica Rasetti, n. sp.
Conococheaguea ovata Rasetti, n. gen., n. sp.
Entomaspis radiatus Ulrich
Idiomesus intermedius Rasetti, n. sp.
Leiocoryphe transversa Rasetti
Plethometopus armatus (Billings)
Plethometopus convergens (Raymond)
Prosaukia stosei (Walcott)
Stenopilus pronus Raymond
Triarthropsis nitida Ulrich

The same assemblage also occurs less commonly in similar limestone beds exposed in the woods a few hundred feet southeast of the quarry. Other, thin limestone beds east of the quarry (loc. cca/3) yielded well-preserved specimens of *Prosaukia stosei.* In some of the layers fragments of *Prosaukia* are silicified and can be etched with hydrochloric acid, but are not as well preserved as the calcareous tests. Poor exposures and structural complication make it difficult to ascertain the relative stratigraphic position of these outcrops, but the differences in horizon are certainly small. Sando collected a cranidium of *Conococheaguea ovata* 0.5 miles N of locality cca (USGS locality 2186).

In the Hagerstown valley of Maryland, the Conococheague formation underlies a considerable area, mapped by Cloos (1941) and in part by Sando (1957). The latter author, in connection with his detailed study of the Lower Ordovician of Maryland, investigated the upper portion of the Conococheague and found that the lithologic boundary between this formation and the overlying Stonehenge limestone does not coincide with the Cambrian-Ordovician boundary, since the Ordovician trilobites *Symphysurina* and *Clelandia* were found to occur 30 feet below the contact as redefined by Sando. According to the previously accepted formational boundary, these fossils would occur about 200 feet below the top of the Conococheague. Hence by any of the suggested limits of the formation, the Conococheague ranges into the Lower Ordovician.

The second locality where relatively numerous Trempealeauian fossils were collected from the upper Conococheague is

just west of Sando's section No. 6, near the Potomac River, in Washington County, Maryland (loc. ccn/2). According to Sando (personal communication) the fossiliferous horizon is approximately 300 feet below the top of the Conococheague as emended by him. The strata show the usual alternation of aphanitic or oölitic, dark-gray limestone and siliceous layers, and numerous beds of intraformational conglomerate are present. All fossils were recovered from small lenses of crystalline limestone in a single, thick bed of aphanitic or finely crystalline limestone. The collections made by Sando and the writer include the species:

Conococheaguea ovata Rasetti, n. gen., n. sp.
Euptychaspis typicalis Ulrich
Idiomesus intermedius Rasetti, n. sp.
Keithiella, sp. undet.
Plethometopus armatus (Billings)
Prosaukia stosei (Walcott)
Stenochilina spinifera Ulrich
Stenopilus, sp. undet.
Triarthropsis limbata Rasetti, n. sp.

At the same locality, a bed of dark-gray, aphanitic limestone 100 feet lower than the one mentioned above yielded numerous fragments of a single species, *Plethometopus obtusus* Rasetti (loc. ccn/1).

The faunule from locality ccn/2 is essentially identical with that occurring in the vicinity of Chambersburg at locality cca. The Maryland locality is important because it establishes the stratigraphic position of this assemblage within the formation.

This faunule includes genera common in most of the Trempealeauian formations of North America (*Plethometopus, Stenopilus, Prosaukia*) and some of more localized occurrence, such as *Bowmania*, described from the Eureka District, Nevada, but occurring in several areas of the central and western United States (A. R. Palmer, personal communication). *Entomaspis* and *Stenochilina* were described from the Eminence dolomite of Missouri, but the former is mentioned by Raasch (1952) as occurring in the upper Mississippi valley and was recently found by Palmer (personal communication) in Nevada. All the other genera, excepting *Conococheaguea* which is unknown elsewhere, were already known from the Appalachian province, chiefly from the boulders in the Levis conglomerate (*Idiomesus, Leiocoryphe, Plethometopus, Stenopilus, Triarthropsis*) and from the Gorge formation of northwestern Vermont (*Idiomesus, Leiocoryphe, Plethometopus, Prosaukia, Stenopilus*). In several instances there is even specific identity between forms of the present faunule and those occurring in the Levis boulders or the Gorge. Many of these genera are also known from the Eminence dolomite of Missouri and from western Newfoundland (Kindle & Whittington, 1958).

This faunal evidence indicates that the strata of the upper Conococheague where the fossils occur are essentially equivalent to some of the Levis boulders and to a portion of the upper Gorge formation. However, it is difficult to decide what part of the Trempealeau is represented by faunules of this type. The trilobites of the type sections of the Trempealeau in the upper Mississippi valley have been inadequately studied (Raasch, 1952), descriptions being mostly confined to the large dikelocephalids and saukiids which are scarce or absent in the Appalachian and western provinces; whereas the smaller trilobites, more useful for correlation with other areas, have been neglected. From a list published by Raasch (1952) it appears that many of the genera characteristic of the Trempealeau range through the entire stage, hence search for short-range genera, and specific discrimination in others, will be required in order to achieve a satisfactory zonation of the Trempealeau. Work now being undertaken by several investigators on the western sections may lead to a satisfactory solution of this problem.

Frederick limestone.—A thin-bedded, dark-gray limestone alternating with irregular, siliceous layers underlies much of the Frederick valley of Maryland. It was named Frederick limestone by Bassler and considered Middle Ordovician. Stose & Stose (1946) suggested on the basis of stratigraphic and paleontologic evidence that the formation is Upper Cambrian. Wilson (1952) reached the same conclusion.

Outcrops of the Frederick limestone are poor, and fossils had so far been collected only from loose slabs in stone walls. The writer was fortunate enough to collect a sizeable trilobite faunule from a small outcrop in the suburbs of Frederick. The exposure is a road cut on East Street and

shows approximately 30 feet of dark-gray, aphanitic limestone in very regular beds 1–2 inches thick, separated by shaly partings but with less siliceous material than is usual in the formation. Most of the fossils came from one 10-inch bed of somewhat more granular limestone 4 feet above the base of the exposed section (loc. ccb/3). The trilobites are mostly of diminutive size and very fragmentary. Nevertheless, careful search yielded over one hundred identifiable specimens. The faunule includes the following species:

Apatokephaloides macrops Rasetti, n. sp.
Aposolenopleura plicata Rasetti, n. sp.
Geragnostus, sp. undet.
Glyptometopus laflammei (Clark)
Keithia intermedia Rasetti, n. sp.
———, sp. undet.
Keithiella cylindrica (Billings)
Loganellus cf. *L. similis* Rasetti
Pseudagnostus gyps (Clark)
Richardsonella unisulcata Rasetti
Theodenisia communis (Rasetti)

Other fossils from the Frederick limestone were collected in loose slabs in stone walls north of the Grove quarry in the eastern suburbs of Frederick (loc. ccm/1). The only trilobite previously described from the formation, "*Acidaspis*" *ulrichi* Bassler, came from this locality. From one slab of aphanitic, dark-gray limestone the writer collected:

Apatokephaloides, sp. undet.
?Bowmania pennsylvanica Rasetti, n. sp.
?Entomaspis radiatus Ulrich
Leiocoryphe cf. *L. brevis*
Litagnostus, sp. undet.
Plethometopus, sp. undet. no. 1
Stenopilus pronus Raymond

This faunal assemblage is similar to the ones occurring in the upper Conococheague at localities cca, ccn/2 and in the Frederick limestone at locality ccb/3. The Trempealeauian fossils from the Frederick limestone show equally strong affinities with the *Hungaia* faunule of the Levis boulders and

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EXPLANATION OF PLATE 51

FIGS. *1–4*—*Plethometopus*, sp. undet. no. 2. *1*, Cranidium, ×5; *2*, Cranidium, ×8; *3*, Pygidium, ×8; *4* Pygidium, ×5 (USNM 136943). Frederick limestone, loc. ccb/3.

5,6—*Onchonotus richardsoni* (Walcott). Dorsal and lateral views of cranidium, ×3 (USNM 136979, plesiotype). Grove limestone, loc. ccb/2.

7—*Litagnostus*, sp. undet. Exfoliated cephalon, ×5 (USNM 136931). Frederick limestone, loc. ccm/1.

8,9—*Lotagnostus* cf. *L. trisectus* (Salter). Cephala, ×5 (USNM 136930). Grove limestone, loc. ccb/2.

10—*Agnostus*, sp. undet. Pygidium, ×8 (USNM 136926), Frederick limestone, loc. ccb/3.

11,12—*Theodenisia communis* (Rasetti). Cranidia, ×8 (USNM 136936, plesiotypes). Frederick limestone, loc. ccb/3.

13,14—*Pseudognostus gyps* (Clark). *13*, Pygidium, ×5; *14*, Cephalon, ×5 (USNM 136929, plesiotypes). Frederick limestone, loc. ccb/3.

15–18—*Geragnostus*, sp. undet. *15*, Cephalon, ×5; *16*, Pygidium, ×5 (USNM 136927). Grove limestone, loc. ccb/2. *17,18*, Pygidia, ×8 (USNM 136928). Frederick limestone, loc. ccb/3.

19–22—*Aposolenopleura plicata* Rasetti, n. sp. *19–21*, Dorsal, frontal, and lateral views of exfoliated cranidium, ×5 (USNM 136980, holotype); *22*, Exfoliated cranidium, ×5 (USNM 136981, paratype). Frederick limestone, loc. ccb/3.

23—*Keithiella cylindrica* (Billings). Exfoliated cranidium, ×3 (USNM 136964, plesiotype). Frederick limestone, loc. ccb/3.

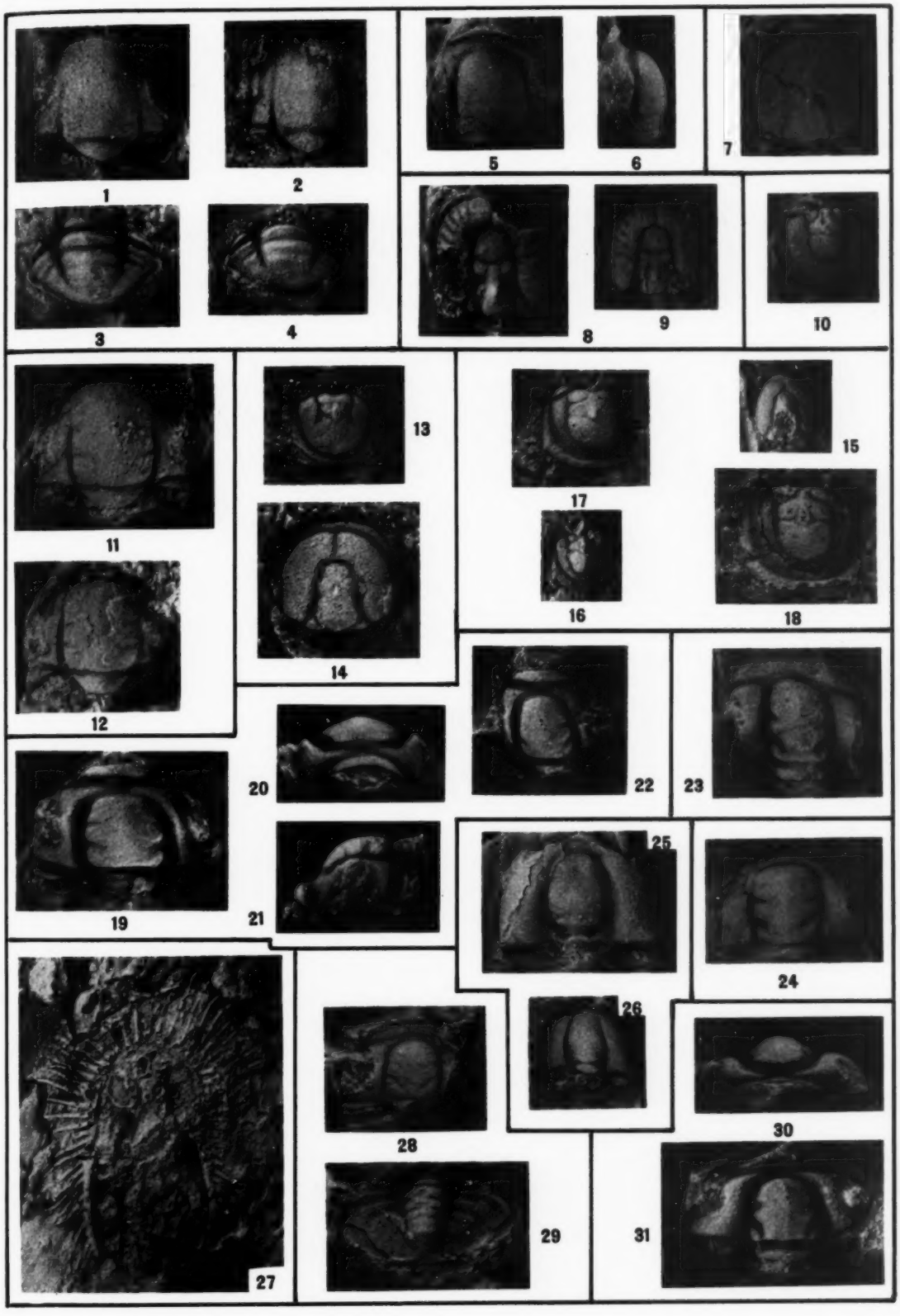
24—*Keithia*, sp. undet. Exfoliated cranidium, ×3 (USNM 136967). Frederick limestone, loc. ccb/3.

25,26—*Idiomesus intermedius* Rasetti, n. sp. *25*, Exfoliated cranidium, ×5 (USNM 136970, holotype). Conococheague limestone, loc. ccn/2. *26*, Cranidium, ×8 (USNM 136971, paratype). Conococheague limestone, loc. cca.

27—"*Acidaspis*" *ulrichi* Bassler. United free cheeks, ×1.5. Frederick limestone, loc. ccm/1 (USNM 136975, plesiotype).

28,29—*Loganellus* cf. *L. similis* Rasetti. *28*, Cranidium, ×3; *29*, Pygidium, ×3 (USNM 136978). Frederick limestone, loc. ccb/3.

30,31—*Glyptometopus laflammei* (Clark). Frontal and dorsal views of exfoliated cranidium, ×8 (USNM 136932, plesiotype). Frederick limestone, loc. ccb/3.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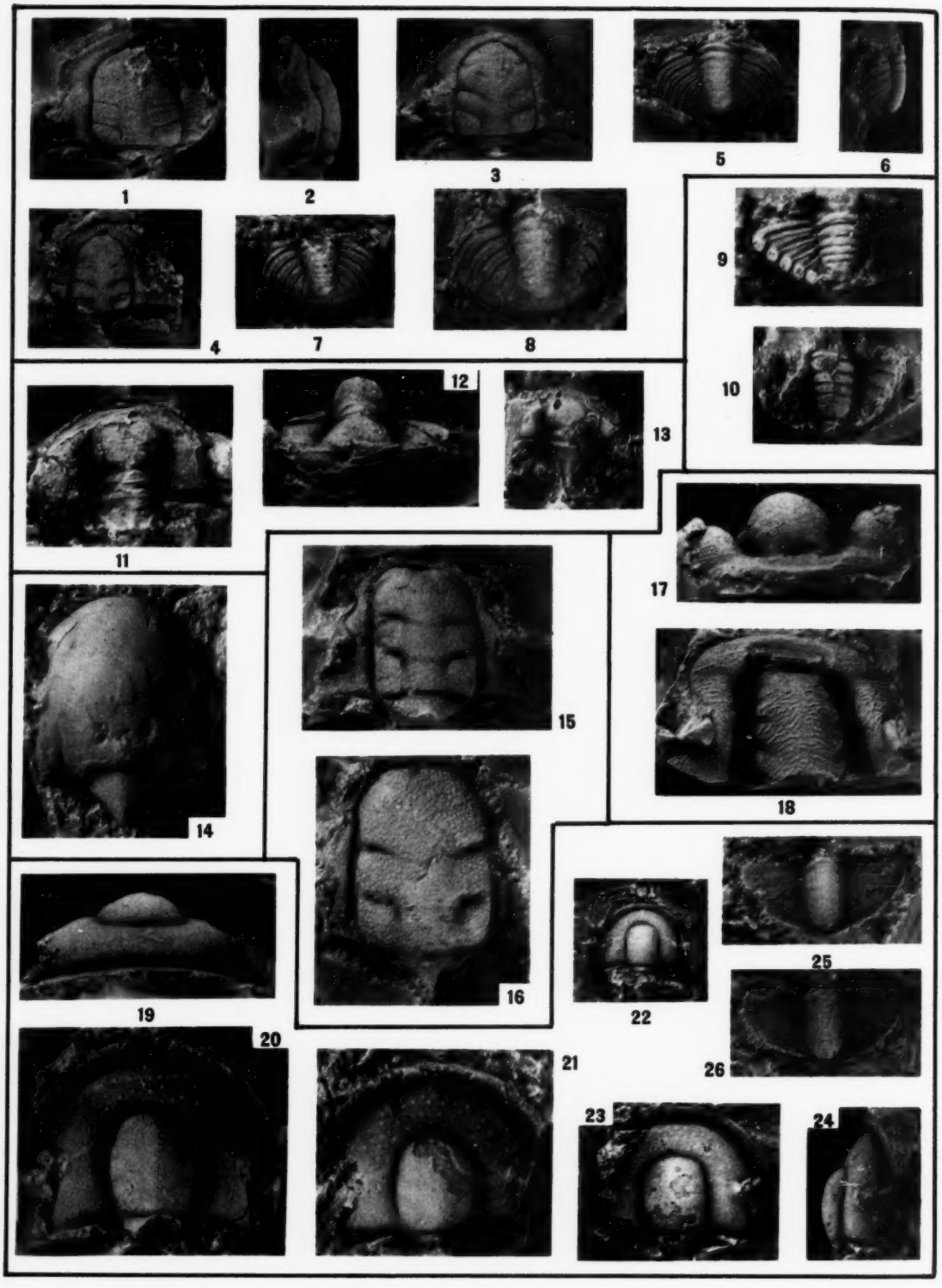
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the Gorge formation as the fossils from the upper Conococheague. Although the precise stratigraphic position of the Trempealeauian fossils in the Frederick limestone is unknown, they may be inferred to occur in the upper part of the formation from the fact that the fossiliferous beds are in close proximity of outcrops of the overlying Grove limestone.

A few fossils were also collected from a small outcrop of Frederick limestone (loc. ccm/2) 0.4 mile SW of locality ccm/1. Here the rock is a thin-bedded, blue-gray limestone alternating with irregular silty layers, typical of the uppermost portion of the formation (Stose & Stose, 1946). The trilobites found here are *Stenopilus* sp., and an undetermined Saukiid.

However, the Frederick limestone is not all of Trempealeauian age as previously assumed. The writer collected a large trilobite faunule from blocks in a stone wall 3.8 miles north of Frederick. These fossils have not been adequately studied, but a preliminary examination definitely shows that they are older than Trempealeauian, presumably either of *Aphelaspis* or post-*Aphelaspis*, pre-*Elvinia* age. The author hopes to be able to describe this faunule in another paper including the Dresbachian and Franconian faunas of the area.

Grove limestone.—In the Frederick valley the Frederick limestone is overlain (Stose & Stose, 1946) by a massive, crystalline, partly dolomitic limestone known as the Grove limestone. This unit has been considered Lower Ordovician on the basis of well-identified brachiopods presumably collected from the upper portion of the formation.

Trilobites were found by the writer for the first time in the Grove limestone at two localities. One is the Ceresville quarry mentioned by Stose & Stose (1946). Here a massive, gray, crystalline limestone about 30–50 feet above the contact with the Frederick limestone yielded poorly preserved but generically identifiable cranidia and pygidia of *Bayfieldia*. A more varied faunule occurred in a loose block of crystalline limestone in a stone wall in the northern suburbs of Frederick (loc. ccb/2). In the pasture immediately west of this stone wall, low outcrops of Grove limestone of identical lithology are seen; these, however, yielded only unidentifiable trilobite fragments. It is highly probable that the loose block came from one of these outcrops. The faunule includes the species:

Apatokephaloides minor Rasetti, n. sp.
Geragnostus, sp. undet.
Hungaia magnifica (Billings)
Leiocoryphe cf. *L. occipitalis* Rasetti
Levisella nasuta Rasetti, n. sp.
Lotagnostus cf. *L. trisectus* (Salter)
Onchonotus richardsoni (Walcott)

EXPLANATION OF PLATE 52

FIGS. *1–8*—*Triarthropsis limbata* Rasetti, n. sp., ×5. *1,2*, Dorsal and lateral views of cranidium (USNM 136934, holotype); *3,4*, Cranidia; *5,6*, Dorsal and lateral views of pygidium; *7,8*, Pygidia (USNM 136935, paratypes). Conococheague limestone, loc. ccn/2.

9,10—*Entomaspis radiatus* Ulrich, ×5. *9*, Pygidium (USNM 136973, plesiotype). Conococheague limestone, loc. cca. *10*, Pygidium tentatively attributed to the species (USNM 136974). Frederick limestone, loc. ccm/1.

11–13—*Euptychaspis typicalis* Ulrich. *11,12*, Dorsal and frontal views of exfoliated cranidium, ×5 (USNM 136968, plesiotype); *13*, Exfoliated cranidium, ×5 (USNM 136969, plesiotype). Conococheague limestone, loc. ccn/2 (specimen of fig. *13* collected by W. J. Sando).

14—*Plethometopus armatus* (Billings). Small cranidium, ×5 (USNM 136937, plesiotype). Conococheague limestone, loc. ccn/2 (see also Pl. 53).

15,16—*Stenochilina spinifera* Ulrich. Cranidia, ×5 (USNM 136988, plesiotypes). Conococheague limestone, loc. ccn/2.

17,18—*Keithiella*, sp. undet. Frontal and dorsal views of cranidium, ×5 (USNM 136989). Conococheague formation, loc. ccn/2.

19–26—*Conococheaguea ovata* Rasetti, n. gen., n. sp., ×5. *19,20*, Frontal and dorsal views of exfoliated cranidium (USNM 136984, holotype); *21,22*, Cranidia; *23,24*, Dorsal and lateral views of cranidium; *25,26*, Pygidia (USNM 136985, paratypes). Conococheague limestone, loc. cca.

Richardsonella megalops (Billings)
——— *subcristata* Rasetti, n. sp.
Theodenisia, sp. undet.

Both the *Bayfieldia* collected in place and the trilobites from the loose block indicate beyond doubt that the lower portion of the Grove formation is Upper Cambrian instead of Lower Ordovician as previously considered. Hence the Cambrian-Ordovician boundary lies somewhere within the formation.

The faunule of the basal Grove limestone is similar in composition to that of the Frederick limestone at locality ccb/3, chiefly differing in the absence of the common genera *Plethometopus* and *Stenopilus*. Analogous differences were observed among the assemblages in individual boulders at Levis (Rasetti, 1944, 1945). For example, the faunule of the Grove limestone is particularly well matched by the assemblage in the author's boulder no. 15 at Levis, while the faunule of the Frederick limestone more closely resembles the assemblage in boulder no. 32. However, so many genera are common to all that the age differences cannot be considerable.

LIST OF LOCALITIES

In the following list the precise position of the localities discussed is indicated by coordinates (x = abscissa, y = ordinate in millimetres) on the USGS topographic maps.

Locality cca—Upper Conococheague limestone; small, abandoned quarry near road north of farmhouse, 2.2 miles S 30°W of Scotland, Franklin Co., Pennsylvania. Coordinates $x=43$, $y=230$, Scotland 7½-minute quadrangle, scale 1:31,680.

Locality ccb/2—Grove limestone; loose block in stone wall on the west side of N. Market Street, opposite 15th Street, in Frederick, Maryland. Coordinates $x=339$, $y=266$, Frederick 7½-minute quadrangle, scale 1:24,000.

Locality ccb/3—Frederick limestone; outcrop on east side of East Street and Pennsylvania R.R. tracks, opposite 14th Street, Frederick, Maryland. Coordinates $x=348$, $y=258$, Frederick 7½-minute quadrangle, scale 1:24,000.

Locality ccb/4—Grove limestone; massive limestone 30–50 feet above the base of the formation at western end of abandoned quarry near Ceresville, Frederick County, Maryland. Coordinates $x=39$, $y=346$, Walkersville 7½-minute quadrangle, scale 1:24,000.

Locality ccm/1—Frederick limestone; loose block in stone wall near limekiln, north of the Grove quarry and south of meat packing plant, in eastern suburbs of Frederick, Maryland. Coordinates $x=382$, $y=124$, Frederick 7½-minute quadrangle, scale 1:24,000.

Locality ccn/2—Upper Conococheague, approximately 300 feet below the top of formation as defined by Sando. Low ridge in pasture 0.25 mile east of Charlton road and 0.1 mile north of Potomac River, in Washington County, Maryland. Coordinates $x=343$, $y=481$, Hedgesville 7½-minute quadrangle, scale 1:24,000.

Locality ccn/1—Same as ccn/2, 100 feet lower stratigraphically.

SYSTEMATIC DESCRIPTIONS

Class TRILOBITA

Family AGNOSTIDAE McCoy, 1846

Genus AGNOSTUS Brongniart, 1822

Type species: *Entomolithus paradoxus pisiformis* Linné.

AGNOSTUS, sp. undet.
Pl. 51, fig. 10

This form is represented by a pygidium. Axis rather short, equidistant from the border laterally and posteriorly, divided into a pair of basal lobes, a median lobe, and a posterior lobe. The latter two are separated by a straight transverse furrow. The median lobe apparently possessed a tubercle. Border moderately wide, marginal spines very small.

This pygidium closely resembles that of *Agnostus orion* Billings from the boulders in the Levis conglomerate.

Occurrence.—Outcrop of Frederick limestone in road cut (loc. ccb/3) in the suburbs of Frederick, Maryland.

Figured specimen.—USNM 136926.

Genus GERAGNOSTUS Howell, 1935

Types species: *Agnostus sidenbladhi* Linnarsson.

GERAGNOSTUS, sp. undet.
Pl. 51, figs. 15–18

A few cephala and pygidia sssociated in a loose block of Grove limestone and several

pygidia from the Frederick limestone are tentatively attributed to the same species.

Glabella not greatly elevated, defined by a shallow dorsal furrow, consisting of the typical parts: basal lobes, anterior, and posterior lobe. Anterior lobe narrower than posterior lobe, rounded in front. Median preglabellar furrows very shallow and seemingly not reaching the border. Border furrow and border of average development.

Pygidium with strongly elevated axis. Axis divided longitudinally into 3 lobes; an elongated tubercle extends through the second lobe and part of the first. Distance from end of axis to border about equal to border width. Border wider than cephalic border; marginal spines small. All specimens are very small.

This form agrees with *Geragnostus* in all characters except possessing a faint preglabellar furrow. In other features it resembles *Geragnostus brevis* Palmer from the Upper Cambrian of Nevada.

Occurrence.—Loose block of Grove limestone (loc. ccb/2) and outcrop of Frederick limestone (loc. ccb/3), both in the suburbs of Frederick, Maryland.

Figured specimens.—USNM 136927–8.

Genus PSEUDAGNOSTUS Jaekel, 1909

Type species: *Agnostus cyclopyge* Tullberg.

PSEUDAGNOSTUS GYPS (Clark)

Pl. 51, figs. 13,14

Plethagnostus gyps CLARK, 1923, p. 124, fig. 9; 1924, p. 16, pl. 3, fig. 2.

Pseudagnostus gyps (Clark). KOBAYASHI, 1939, p. 158.

Pseudagnostus gyps (Clark). RASETTI, 1944, p. 234, pl. 36, figs. 20–22.

Cephala and pygidia do not significantly differ from specimens from the type locality, the boulders in the Levis conglomerates.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Types.—Plesiotypes: USNM 136929.

Genus LOTAGNOSTUS Whitehouse, 1936

Type species: *Agnostus trisectus* Salter.

LOTAGNOSTUS cf. L. TRISECTUS (Salter)

Pl. 51, figs. 8,9

Agnostus trisectus SALTER, 1864, p. 10, pl. 1, fig. 11.

Lotagnostus trisectus (Salter). WHITEHOUSE, 1936, p. 101.

Lotagnostus trisectus (Salter). RASETTI, 1945a, p. 463, pl. 60, fig. 1.

Lotagnostus trisectus (Salter). HUTCHINSON, 1952, p. 70, pl. 1, figs. 6–12.

Two cephala seem to agree with the species in all respects; unfortunately no pygidia were collected.

Occurrence.—Loose block of Grove limestone (loc. ccb/2) in the suburbs of Frederick, Maryland.

Figured specimens.—USNM 136930.

Genus LITAGNOSTUS Rasetti, 1944

Type species: *Litagnostus levisensis* Rasetti.

LITAGNOSTUS, sp. undet.

Pl. 51, fig. 7

A cephalon and a pygidium of this genus were collected. The cephalon is exfoliated and shows exceedingly shallow furrows of the *Pseudagnostus* type; presumably the outer surface would appear completely smooth except for the border furrow and border which are well developed. The pygidium is seemingly smooth but for the presence of a border wider than in the cranidium.

Occurrence.—Loose block of Frederick limestone (loc. ccm/1) in the suburbs of Frederick, Maryland.

Figured specimen.—USNM 136931.

Family LONCHOCEPHALIDAE Hupé, 1953

Genus GLYPTOMETOPUS Rasetti, 1944

Type species: *Solenopleura laflammei* Clark.

GLYPTOMETOPUS LAFLAMMEI (Clark)

Pl. 51, figs. 30,31

Solenopleura laflammei CLARK, 1924, p. 26, pl. 3, fig. 7.

Glyptometopus laflammei (Clark). RASETTI, 1944, p. 421, pl. 36, fig. 53; 1945a, p. 467, pl. 61, figs. 1,2.

Two cranidia seem to represent this species, previously known only from boulders in the Levis conglomerates.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Types.—Plesiotype: USNM 136932.

Family CATILLICEPHALIDAE Raymond, 1938

Genus TRIARTHROPSIS Ulrich, 1930

Type species: *Triarthropsis nitida* Ulrich.

TRIARTHROPSIS NITIDA Ulrich
Pl. 55, figs. 6–13

Triarthropsis nitida ULRICH in BRIDGE, 1930, p. 214, pl. 19, figs. 3,4.
Triarthropsis nitida Ulrich. RASETTI, 1954, p. 607, text-fig. 2d.

Several cranidia and free cheeks recovered from the upper Conococheague formation seem identical with the types from the Eminence dolomite of Missouri. The cranidium from which the author's previous illustration was made is somewhat nontypical in being proportionately shorter and wider than the type specimens; it was chosen because of the preservation of the complete posterior area, which was broken off in Ulrich's specimens and is represented too short in his illustrations.

Pygidium attributed to the species about twice wider than long, of high convexity. Axis rising above the pleural lobes, tapered, rounded posteriorly, almost reaching the posterior margin, showing 6 or 7 rings defined by furrows only at the sides. Pleural lobes entirely convex, without border furrow or border. Five pairs of pleural furrows, of decreasing depth, extending almost to the margin, alternating with narrower and shallower but very distinct interpleural grooves. Margin entire, possibly excepting a slight serration in correspondence of the first two or three pleural segments. Axis with a row of 4 regularly arranged tubercles on each ring; scattered tubercles of the same size occur on the pleural lobes. Length of largest pygidium 3.5 mm., width 6 mm.

This pygidium differs considerably from the one attributed to *Triarthropsis marginata* (Rasetti) in being wider and shorter and in possessing a greater number of segments. The two pygidia have in common the very low degree of fusion of the pleural segments. The assignment is made very probable by the similarity of this pygidium to the one described for the following species, *T. limbata.*

Occurrence.—Conococheague formation (loc. cca), Franklin County, Pennsylvania.

Types.—Plesiotypes: USNM 136933.

TRIARTHROPSIS LIMBATA Rasetti, n. sp.
Pl. 52, figs. 1–8

Available material.—Numerous, well-preserved cranidia and pygidia.

Description.—Glabella moderately convex, not rising above the general convexity of the cephalon, defined by narrow, but well marked dorsal furrow. Glabella almost straight-sided, slightly tapered, somewhat pointed in front. First pair of glabellar furrows short and shallow, starting from the dorsal furrow and curving inward and forward. Furrows of second pair in form of very shallow, short pits not connected with dorsal furrow. Furrows of third and fourth pairs starting from the dorsal furrow, directed obliquely inward and backward; those of fourth pair sharply turning backward after crossing one-third of the glabellar width and almost isolating basal glabellar lobes. A faint median indentation on frontal glabellar lobe. Occipital furrow straight; occipital ring very short (sag.), tapered laterally, with a small median node. Fixed cheeks moderately downsloping; frontal area relatively long (sag.) for the genus, faintly divided into narrow (sag.) border and wider preglabellar field by indistinct border furrow. Palpebral area about one-fifth as wide as glabella; palpebral lobes about one-fourth the glabellar length, set off by indistinct palpebral furrow. Anterior facial sutures divergent in front of eyes, producing greater lateral extension of frontal area than usual in the genus. Posterior branch curving outward and backward, producing long (tr.), slender, well furrowed posterior area. Surface of cranidium very finely granulated.

Pygidium attributed to the species by close association with cranidium. Axis slightly tapered, very prominent, showing about 6 rings and a terminal section, rounded posteriorly, reaching four-fifths of the pygidial length. Pleural lobes entirely convex, downsloping. Six pleural furrows and 5 interpleural grooves visible on most specimens; furrows narrow but well marked, becoming obsolete before reaching the margin; grooves on the contrary very shallow proximally, becoming more pronounced distally where the furrows disappear, reaching the margin. Border furrow and border lacking. Margin entire with rather uniform curvature. Test very finely granulated; in addition there are a few scattered, low tubercles on the pleural lobes, and somewhat indistinct, paired tubercles on the axial rings.

Length of largest cranidium 4 mm., of largest pygidium 3 mm.

Remarks.—This species is very similar to *T. nitida* but differs consistently in a number of characters. The glabella is proportionately shorter and wider; the dorsal and glabellar furrows are shallower; the frontal area is considerably longer and wider; the pygidium has a relatively shorter axis and less distinct axial nodes.

Occurrence.—Conococheague formation (loc. ccn/2), Washington County, Maryland.

Types.—Holotype: USNM 136934. Paratypes: USNM 136935.

Genus STENOCHILINA Ulrich, 1930

Type species: *Stenochilina spinifera* Ulrich.

STENOCHILINA SPINIFERA Ulrich

Pl. 52, figs. 15,16

Stenochilina spinifera ULRICH in BRIDGE, 1930, p. 215, pl. 19, figs. 1,2.

Two cranidia from the Conococheague formation appear identical with the types from the Eminence dolomite of Missouri.

Occurrence.—Conococheague formation (loc. ccn/2), Washington County, Maryland.

Types.—Plesiotypes: USNM 136988.

Genus THEODENISIA Clark, 1948

Type species: *Denisia eminens* Clark.

THEODENISIA COMMUNIS (Rasetti)

Pl. 51, figs. 11,12

Acheilus communis RASETTI, 1944, p. 237, pl. 36, figs. 29,30.

Theodenisia communis (Rasetti). RASETTI, 1954, p. 609, text-fig. 3b.

A species of *Theodenisia* which is relatively common in the Frederick limestone is identified with *T. communis* from the Levis boulders. The cranidia from Maryland show some variability in the shape of the glabella and the depth of the glabellar furrows like the specimens from the type locality.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Types.—Plesiotypes: USNM 136936.

Family PLETHOPELTIDAE Raymond, 1924

Genus PLETHOMETOPUS Ulrich, 1930

Type species: *Bathyurus armatus* Billings.

PLETHOMETOPUS ARMATUS (Billings)

Pl. 53, figs. 1–8; Pl. 52, fig. 14

Bathyurus armatus BILLINGS, 1860, p. 319, fig. 23; in LOGAN, 1863, p. 238, fig. 273; 1865, p. 411, fig. 392.

Plethopeltis armata (Billings). RAYMOND, 1913, p. 65, pl. 7, fig. 18.

Plethometopus armatus (Billings), ULRICH in BRIDGE, 1930, p. 221.

Plethometopus armatus (Billings). RASETTI, 1944, p. 251, pl. 39, fig. 25.

A species of *Plethometopus* which does not appear to differ significantly from the type of *P. armatus* is common in the Conococheague at several localities. All the cranidia collected are much smaller than the holotype which, however, is of exceptional size also among the specimens from the type locality at Levis, Quebec.

Pygidia unquestionably belonging to the species are figured. They are essentially identical with unassigned pygidia from the Levis conglomerate figured by the author (Rasetti, 1945a, pl. 62, figs. 32,33,36,37). These pygidia also belong to species of *Plethometopus*, either *P. armatus* or similar associated species.

Occurrence.—The figured specimens are from the Conococheague formation at locality cca, Franklin Co., Pennsylvania, and locality ccn/2, Washington County, Maryland.

Types.—Plesiotypes: USNM 136937–8.

PLETHOMETOPUS OBTUSUS Rasetti

Pl. 53, figs. 11–14

Plethometopus obtusus RASETTI, 1945a, p. 472, pl. 62, figs. 1,2.

Unassigned pygidium no. 7, RASETTI, 1945a, p. 477, pl. 62, figs. 29,30.

A large form of *Plethometopus* occurring at several localities in the Conococheague formation is referred to this species. In certain beds this is the only fossil. The pygidium had already been described and figured by the writer from the Levis boulders but had not been referred to a cranidium. At that locality it also occurs in association with the cranidia of *P. obtusus*.

The test has a characteristic ornamentation, mainly consisting of irregular terrace lines, covering the entire surface of the free cheeks and pygidium, and less markedly some portions of the cranidium, in particular the frontal and posterior areas. On the

free cheeks, the areas between the anastomosing terrace lines are punctate. The largest complete cranidium has a length of 24 mm. The anterior facial sutures are more strongly divergent in small cranidia, as may be seen on the two figured specimens.

Occurrence.—Upper Conococheague formation at Wilson's locality 47-29w-3 near Big Spring Station, and author's locality ccn/1, both in Washington County, Maryland.

Types.—Plesiotypes: USNM 136939–40.

PLETHOMETOPUS CONVERGENS (Raymond)
Pl. 53, figs. 15–19

Plethopeltis convergens RAYMOND, 1924, p. 419, pl. 13, fig. 2.
Plethometopus convergens (Raymond). ULRICH in BRIDGE, 1930, p. 221.
Plethometopus convergens (Raymond). RASETTI, 1944, p. 251, pl. 39, fig. 27.

Several cranidia recovered from the Conococheague formation seem identical with the type from the Gorge formation and specimens from the Levis boulders. As usual, only the smaller cranidia are relatively well preserved, but fragments indicate that the species attains a rather large size. One imperfect cranidium has a length of almost 30 mm.

Several pygidia were found in close association and almost certainly belong to the species. Like the cranidium, the pygidium partakes of the characters of *Plethometopus* and *Stenopilus*. Pygidium 1.4 times wider than long, essentially convex in all directions. Axis only marked by a pair of rather deep notches on the anterior margin, otherwise merging with the pleural lobes. Articulating ring expanded medially; a median tubercle rises immediately behind the articulating furrow. Anterior outline of pleural lobes truncated by facets inclined at about 45°. Posterior outline semi-elliptical with maximum curvature at the posterior end. Longitudinal profile convex, the curvature increasing rearward; transverse profile convex with maximum curvature on midline. Entire surface of pygidium covered with irregular, transverse terrace lines.

This pygidium differs from all the known pygidia of *Plethometopus* in the almost complete fusion of the axis with the pleural lobes and the convexity of the entire surface. In both characters it resembles the pygidia of *Stenopilus*, except that the latter are much narrower and longer, as a consequence of the almost longitudinal course of the facets of the pleural lobes. The largest pygidium is 11 mm. long and 15 mm. wide.

Occurrence.—Conococheague formation (loc. cca), Franklin County, Pennsylvania.

Types.—Figured plesiotypes: USNM 136941.

PLETHOMETOPUS, sp. undet. no. 1
Pl. 53, figs. 9,10

Cranidia and pygidia of a species of *Plethometopus* were recovered from a loose block of Frederick limestone. The cranidium is very much like *P. armatus* except that the occipital ring is shorter and does not extend into a long spine. In this feature the cranidium resembles *P. obtusus*, differing in the lesser divergence of the anterior facial sutures and the proportionately wider glabella. The associated pygidium is almost identical with *P. armatus* and quite different from *P. obtusus*.

Occurrence.—Loose block of Frederick limestone (loc ccm/1) in the suburbs of Frederick, Maryland.

Figured specimens.—USNM 136942.

PLETHOMETOPUS, sp. undet. no. 2
Pl. 51, figs. 1–4

A species of *Plethometopus* is by far the most common fossil in the Frederick limestone at locality ccb/3. However, only small, evidently immature cranidia, free cheeks and pygidia were recovered in fairly good state of preservation. Although this form cannot be identified with described species, it is not deemed proper to name a species on such immature material.

The cranidium does not differ significantly from *Plethometopus armatus*, except in the lesser length and more obtuse shape of the occipital ring. The pygidium, however, is quite different, rather resembling *P. obtusus*. The axis is long and merges posteriorly with the steep slope of the pleural lobes, as in *P. obtusus*, but is narrower in proportion to the pleural lobes than in that species.

Occurrence.—Frederick limestone (locality ccb/3), road cut in the suburbs of Frederick, Maryland.

Figured specimens.—USNM 136943.

Genus STENOPILUS Clark, 1924

Type species: *Stenopilus intermedius* Clark.

The designation of the author and type species of the genus *Stenopilus* requires an explanation. Raymond (1924) described the genus as new, designating as type species *Stenopilus pronus* Raymond. Raymond's publication appeared in July 1924. However, in a paper issued in June 1924, Clark (1924) had inadvertently proposed *Stenopilus* as a monotypic genus by describing a species, *Stenopilus intermedius*. Thus the genus must be credited to Clark, contrary to common usage, and the type species is selected accordingly. The two species are very close to each other and obviously congeneric.

STENOPILUS PRONUS Raymond
Pl. 53, figs. 20–24

Stenopilus pronus RAYMOND, 1924, p. 420, pl. 13, figs. 6,7.

This species, common at the type locality in the Gorge formation of Vermont, is also abundant at the Scotland locality in the upper Conococheague. A few specimens were also recovered from the Frederick limestone. Both the cranidia and pygidia (the latter not described before) are identical with the Vermont specimens.

The pygidium is essentially identical with that of *Stenopilus elongatus* described by the writer (1945b) except for the much larger size. The cranidia from the Conococheague limestone attain the largest size over observed in this species. The largest specimen collected is an incomplete cranidium 32 mm. wide which, if complete, would be 40 mm. long.

Occurrence.—Conococheague formation (loc. cca), Franklin Co., Pennsylvania. Also from a loose block of Frederick limestone (loc. ccm/1) in the suburbs of Frederick, Maryland.

Types.—Plesiotypes: USNM 136944–5.

Genus LEIOCORYPHE Clark, 1924

Type species: *Leiocoryphe gemma* Clark.

LEIOCORYPHE cf. L. GEMMA Clark
Pl. 53, fig. 32

Leiocoryphe gemma CLARK, 1924, p. 21, pl. 3, fig. 8.

Leiocoryphe gemma Clark, RASETTI, 1944, p. 245, pl. 38, figs. 1,2.

A single cranidium collected resembles this species. It differs from specimens from the type locality in the lesser convexity and lesser rearward expansion of the occipital ring.

Occurrence.—Frederick limestone (loc. ccm/1), loose block in the suburbs of Frederick, Maryland.

Figured specimen.—USNM 136946.

LEIOCORYPHE TRANSVERSA Rasetti
Pl. 53, figs. 25–30

Leiocoryphe n. sp., RASETTI, 1945b, p. 120, pl. 1, figs. 5,6,8,9.
Leiocoryphe transversa RASETTI, 1945a, p. 469, pl. 61, fig. 9.

Several cranidia of *Leiocoryphe* appear identical with the types. In addition, a pygidium almost certainly belonging to this species and a free cheek were collected. Search among the author's collections from the boulders in the Levis conglomerate revealed an identical pygidium, found in boulder no. 32 where the cranidia of the species are common.

The new material supplies additional information about the species. The pygidium has a very simple structure. It is flat, smooth, about 3 times wider than long with almost straight anterior outline. Axis barely indicated by a slight elevation of the median portion and by the presence of the articulating ring and furrow. Posterior margin downfolded into a vertical doublure marked by terrace lines; these lines extend for a short distance onto the dorsal surface.

Free cheeks were previously known, complete cephala occurring at Levis. However, on such specimens the author had been unable to detect the presence of a median suture between the doublures of the free cheeks (Rasetti, 1952, p. 892). The separated free cheek illustrated herein shows the median suture very clearly. Subsequently this character was observed also in cephala from the type locality. It thus appears that a median (asaphid) suture is the rule in the species of *Leiocoryphe*, as in the related genera *Plethometopus* and *Stenopilus*.

Occurrence.—The specimens figured herein are from boulder no. 32 in the Levis conglomerate at Levis, Quebec and from the

Conococheague formation (loc. cca), Franklin Co., Pennsylvania.

Types.—Plesiotypes figured herein: USNM 136947–48.

LEIOCORYPHE cf. L. OCCIPITALIS Rasetti
Pl. 53, fig. 31

Leiocoryphe occipitalis RASETTI, 1944, p. 245, pl. 38, fig. 4.

A few, small cranidia resemble this species, differing only in the shallower occipital furrow and less expanded occipital ring.

Occurrence.—Grove limestone (loc. ccb/2), loose block in the suburbs of Frederick, Maryland.

Figured specimen.—USNM 136949.

Family REMOPLEURIDIDAE
Hawle & Corda, 1847
Subfamily RICHARDSONELLINAE
Raymond, 1924
Genus RICHARDSONELLA
Raymond, 1924

Types species: *Dikelocephalus megalops* Billings.

RICHARDSONELLA MEGALOPS (Billings)
Pl. 55, fig. 14

Dikelocephalus megalops BILLINGS, 1860, p. 311, fig. 9; in LOGAN, 1863, p. 236, fig. 257; 1865, p. 403, fig. 380.
Conokephalina megalops (Billings). WALCOTT, 1914, p. 351.
Richardsonella megalops (Billings). RAYMOND, 1924, p. 438.
Richardsonella megalops (Billings). RASETTI, 1944, p. 255, pl. 39, figs. 48,49.

A cranidium seems to represent this species. Although not too well preserved, the specimen shows the "fingerprint" ornamentation characteristic of several species of the genus.

Occurrence.—Loose block of Grove limestone (loc. ccb/2) in the suburbs of Frederick, Maryland.

Types.—Plesiotype: USNM 136950.

RICHARDSONELLA SUBCRISTATA
Rasetti, n. sp.
Pl. 55, figs. 15–18

Available material.—Several cranidia, free cheeks, and pygidia moderately well preserved in limestone.

Description.—Cranidium typical of the genus. Glabella slightly tapered in the posterior two-thirds, parallel-sided in the anterior third, weakly convex longitudinally, rather convex transversely especially

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EXPLANATION OF PLATE 53

FIGS. *1–8*—*Plethometopus armatus* (Billings). *1,2*, Dorsal and lateral views of cranidium, ×3; *3*, Pygidium, ×3; *4*, Free cheek, ×5; *5,6*, Dorsal and lateral views of pygidium, ×5; *7*, Pygidium with unusually strong furrows on pleural lobes, ×5; *8*, Cranidium, ×3 (USNM 136938, plesiotypes). Conococheague limestone, loc. cca.

9,10—*Plethometopus*, sp. undet. no. 1, *9*, Cranidium, ×2; *10*, Pygidium, ×3 (USNM 136942). Frederick limestone, loc. ccm/1.

11–14—*Plethometopus obtusus* Rasetti. *11*, Small cranidium, ×5 (USNM 136939, plesiotype, collected by J. L. Wilson). Conococheague limestone, loc. 47-29W-3. *12*, Large cranidium, ×1; *13*, Pygidium, ×5; *14*, Portion of marginal surface of free cheek, ×5, showing peculiar ornamentation (USNM 136940), plesiotypes. Conococheague limestone, loc. ccn/1.

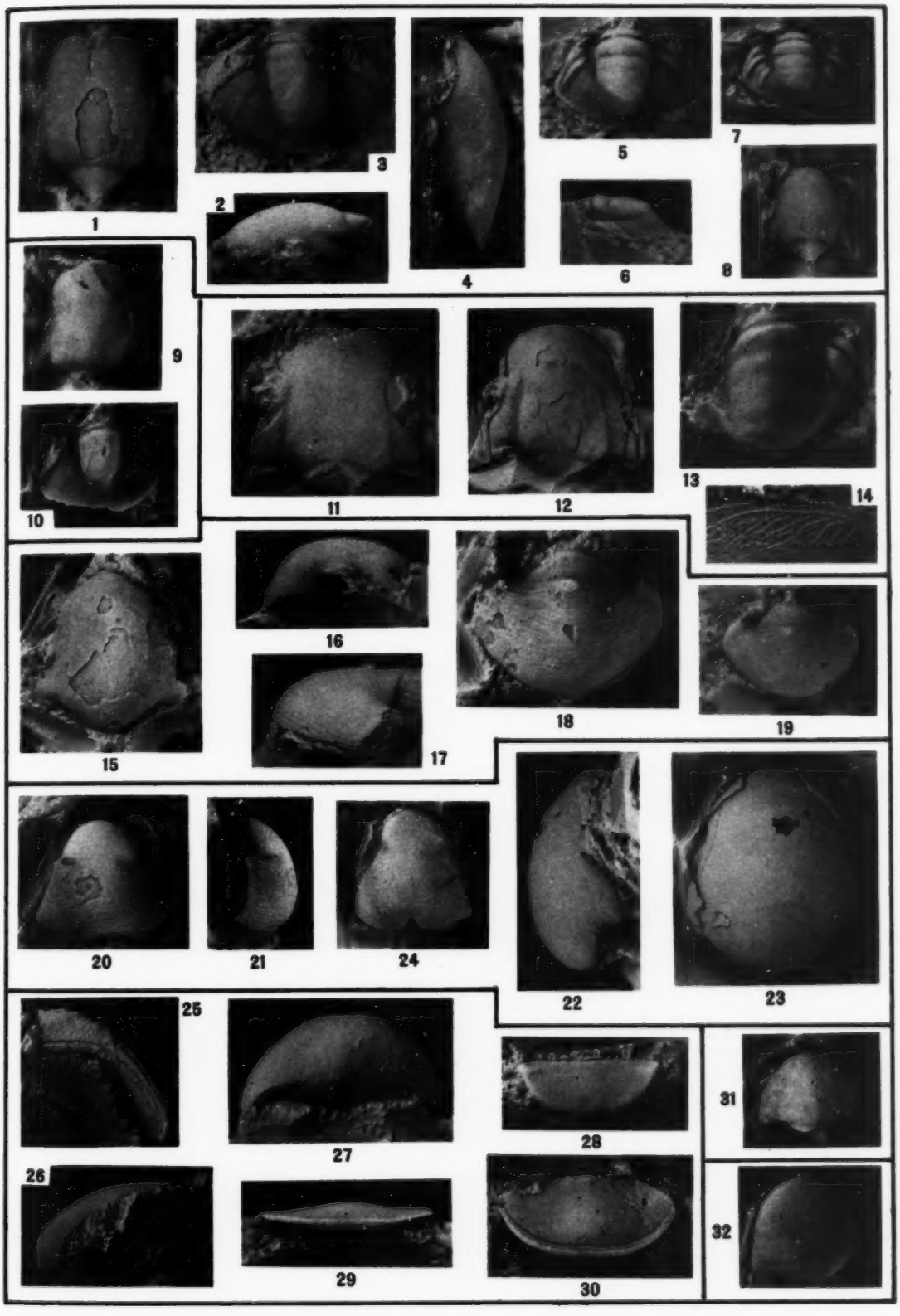
15–19—*Plethometopus convergens* (Raymond). *15,16*, Dorsal and lateral views of cranidium, ×3; *17,18*, Lateral and dorsal views of pygidium, ×5; *19*, Pygidium, ×3 (USNM 136941, plesiotypes). Conococheague limestone, loc. cca.

20–24—*Stenopilus pronus* Raymond. *20,21*, Posterior and lateral views of small pygidium, ×5; *22,23*, Lateral and dorsal views of exfoliated cranidium, ×3 (USNM 136944, plesiotypes). Conococheague limestone, loc. cca. *24*, Posterior view of exfoliated pygidium, ×2 (USNM 136945, plesiotype). Frederick limestone, loc. ccm/1.

25–30—*Leiocoryphe transversa* Rasetti, ×8. *25,26*, Antero-ventral and dorsal views of left free cheek; *27*, Cranidium; *28*, Pygidium (USNM 136947, plesiotypes). Conococheague limestone, loc. cca. *29,30*, Posterior and dorsal views of pygidium (USNM 136948, plesiotype). Boulder no. 32 in Levis conglomerate, Guay's quarry, Levis, Quebec.

31—*Leiocoryphe* cf. *L. occipitalis* Rasetti. Cranidium, ×8 (USNM 136949). Grove limestone, loc. ccb/2.

32—*Leiocoryphe* cf. *L. gemma* Clark. Cranidium, ×5 (USNM 136946). Frederick limestone, loc. ccm/1.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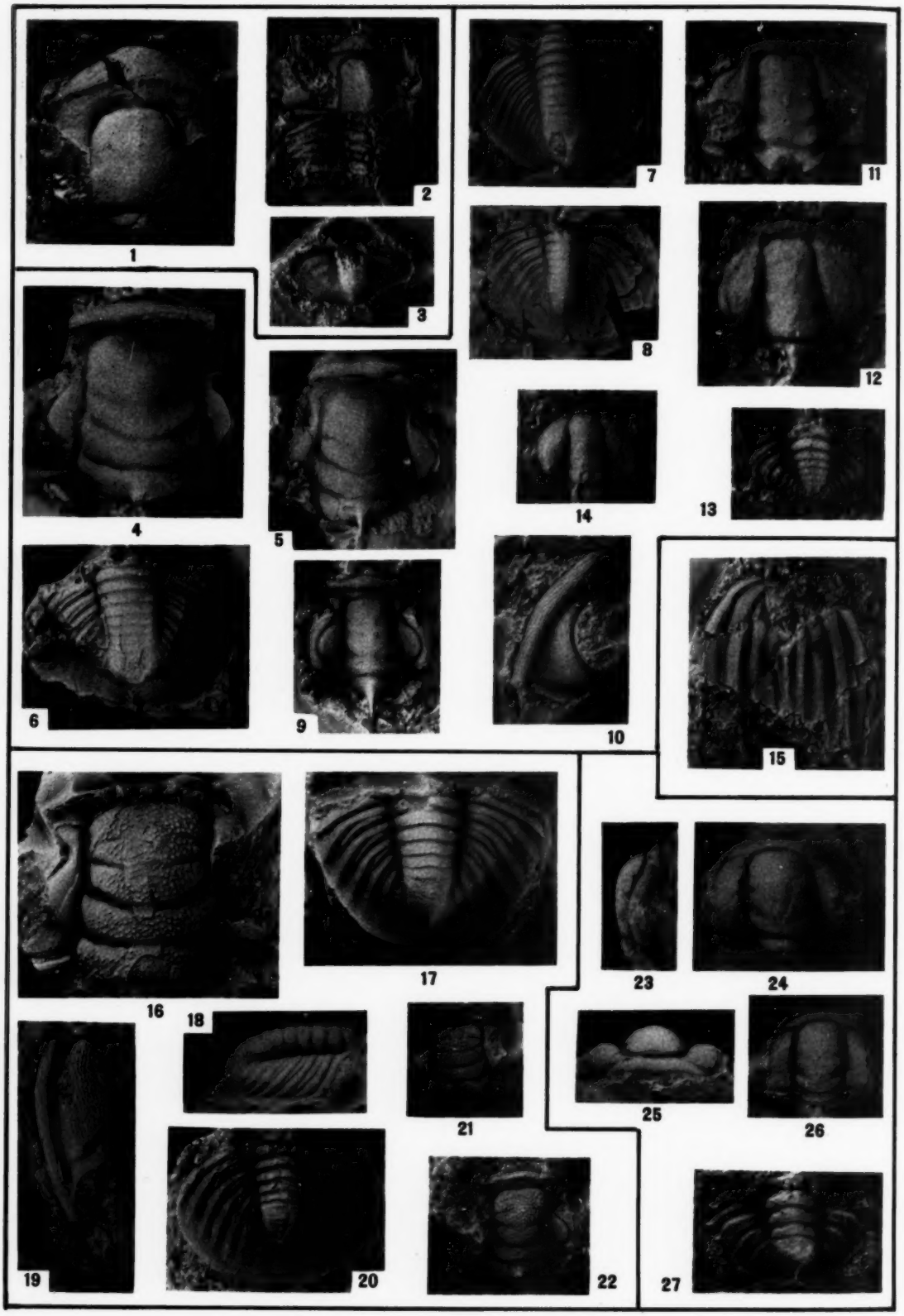
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in the posterior portion which shows a prominent keel, dropping steeply down to well-impressed occipital furrow. Posterior pair of glabellar furrows well impressed, two other pairs very shallow. Palpebral area reduced to a narrow, convex strip between the dorsal furrow and the palpebral furrow. Palpebral lobes large, semicircular, as in the type species. Preglabellar field very short (sag.), equaling the width (sag.) of the border. Anterior marginal furrow deep, marked by the usual series of puncta. Posterior area not preserved. Anterior facial suture in the dorsal furrow immediately in front of the eyes, then diverging at an angle of about 60°, forming sharp anterior angles of the cranidium. Incomplete free cheeks indicate the usual advanced position of the genal spine. Surface of test with usual "fingerprint" ornamentation. Length of largest cranidium 9 mm.

Pygidium with elevated, slightly tapered axis showing three rings and a terminal section, extended into a postaxial ridge. Axis occupying about two-thirds of the pygidial length. Pleural lobes flat; pleural furrows shallow, curving backward; pleura extended into three or possibly four pairs of flat spines of decreasing length. Surface ornamented like the cranidium.

Remarks.—This form is intermediate between two of the species of the Levis boulders, *R. cristata* (Billings) and *R. unisulcata* Rasetti. The former has obsolete glabellar furrows and a more strongly keeled glabella; in the latter species the dorsal and glabellar furrows are less deeply impressed than in *R. subcristata* and the glabella is flat like in *R. megalops*. The pygidium is similar to that of *R. unisulcata*.

Occurrence.—Loose block of Grove limestone (loc. ccb/2) in the suburbs of Frederick, Maryland.

Types.—Holotype: USNM 136951. Paratypes: USNM 136952.

Richardsonella cf. R. unisulcata Rasetti

Pl. 55, fig. 19

Richardsonella unisulcata Rasetti, 1944, p. 256, pl. 39, figs. 54–46.

A few cranidia agree with the types of this species but are too poorly preserved to allow a positive identification.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Figured specimen.—USNM 136953.

Genus Apatokephaloides Raymond, 1924

Type species: *Apatokephaloides clivosus* Raymond.

Apatokephaloides minor Rasetti, n. sp.

Pl. 55, figs. 29–32

Available material.—Several moderately well-preserved cranidia.

Description.—Glabella large, moderately

Explanation of Plate 54

Figs. *1–3*—*Levisella nasuta* Rasetti, n. sp. *1*, Exfoliated cranidium, ×3 (USNM 136976, holotype); *2*, Cranidium with several thoracic segments, ×5; *3*, Exfoliated pygidium, ×5 (USNM 136977, paratypes). Grove limestone, loc. ccb/2.

4–14—*Prosaukia corrugata* Rasetti, n. sp. *5*, Exfoliated cranidium, ×1 (USNM 136962, holotype); *4*, Exfoliated cranidium, ×2; *6*, Exfoliated pygidium, exposing impression of doublure, ×3; *7*, Immature pygidium, ×5; *8*, Exfoliated pygidium, ×1; *9*, Small cranidium, ×5; *10*, Small free cheek, ×5; *11,12,14*, Meraspid cranidia, ×20; *13*, Transitory pygidium, ×20. (USNM 136963, paratypes). Conococheague limestone, loc. cca/1.

15—*Hungaia magnifica* (Billings). Pygidium, ×3 (USNM 136958). Grove limestone, loc. ccb/2.

16–22—*Prosaukia stosei* (Walcott). *16*, Exfoliated cranidium, ×2; *17,18*, Dorsal and lateral views of pygidium, ×3 (USNM 136960), plesiotypes. Conococheague limestone, loc. cca/3. *19*, Free cheek, ×1; *20*, Pygidium, ×2; *21,22*, Cranidia, ×2 (USNM 136961, plesiotypes). Conococheague limestone, loc. cca.

23–27—*Keithia intermedia* Rasetti, n. sp. *23–25*, Lateral, dorsal, and frontal views of exfoliated cranidium, ×3 (USNM 136965, holotype); *26*, Exfoliated cranidium, ×3; *27*, Exfoliated pygidium, ×5 (USNM 136966, paratypes). Frederick limestone, loc. ccb/3.

convex, well defined by the dorsal furrow, slightly tapered, rounded in front. Posterior glabellar furrows short, oblique, rather shallow; another pair of similar character but less impressed. Occipital furrow straight, well impressed throughout; occipital ring rather long (sag.). Palpebral area reduced to a narrow strip between the palpebral furrow and the dorsal furrow; palpebral lobes about half the glabellar length, moderately curved, flat. Pre-glabellar field short (sag.); anterior marginal furrow well marked, with indistinct puncta; anterior border raised, as wide (sag.) medially as the preglabellar field. Anterior facial sutures moderately divergent. Posterior area and sutures not preserved. Surface finely and indistinctly granulated. Length of largest cranidium 5 mm.

Remarks.—This species is closest to *Apatokephaloides pauper* (Billings) from the Levis boulders. It differs mainly in the smaller size, shallower glabellar furrows, more distinct palpebral furrow, long (sag.) frontal area, and wider and less elevated anterior border.

Occurrence.—Loose block of Grove limestone (loc. ccb/2) in the suburbs of Frederick, Maryland.

Types.—Holotype: USNM 136954. Paratypes: USNM 136955.

APATOKEPHALOIDES MACROPS
Rasetti, n. sp.
Pl. 55, figs. 24–28

Available material.—Two fairly well preserved cranidia, and one pygidium tentatively attributed to the species.

Description.—The cranidium of this species is so similar to the preceding that it seems sufficient to list the differences. The anterior facial sutures are less divergent; the palpebral lobes are longer, being distinctly longer than half the glabella, and somewhat more posteriorly located, their posterior ends almost attaining the level of the occipital furrow. The posterior area is preserved in one specimen and has the same shape and proportionate size as in *A. pauper*. One cranidium is exfoliated and appears smooth, the other preserves the test and shows an indistinct granulation. Length of larger cranidium 4.5 mm.

The pygidium tentatively assigned to the species has a very prominent axis composed of 2 rings and a terminal section with a pair of strong tubercles. The axis does not reach the posterior margin and is followed by a low postaxial ridge. The pleural lobes have little convexity and show 3 pairs of pleural furrows and two pairs of interpleural grooves almost reaching the margin, which is not well preserved but seems denticulated. There is no marginal furrow or border. Length of pygidium 2.5 mm., width 4.5 mm. This pygidium resembles those of other members of the Richardsonellinae. No pygidium has been definitely assigned to any of the known species of *Apatokephaloides*.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Types.—Holotype: USNM 136956. Paratypes: USNM 136957.

Family HUNGAIIDAE Raymond, 1924
Genus HUNGAIA Walcott, 1914

Type species: *Dikelocephalus magnificus* Billings.

HUNGAIA MAGNIFICA (Billings)
Pl. 54, fig. 15

Dikelocephalus magnificus BILLINGS, 1860, p. 307, fig. 5; in LOGAN, 1863, p. 235, figs. 255a,b; 1865, p. 399, fig. 376.
Apatokephalus magnificus (Billings). BROEGGER, 1897, p. 175, fig. 10.
Hungaia magnifica (Billings). WALCOTT, 1914, p. 351.
Hungaia magnifica (Billings). RASETTI, 1944, p. 242, pl. 37, figs. 1–3.

Two incomplete pygidia, lacking the axis, agree in all observable features with typical material of the species, previously known exclusively from the boulders in the Levis conglomerate.

Occurrence.—Loose block of Grove limestone (loc. ccb/2) in the suburbs of Frederick, Maryland.

Types.—Figured plesiotype: USNM 136958.

Family EUREKIIDAE Hupé, 1952
Genus BAYFIELDIA Clark, 1924

Type species: *Bayfieldia tumifrons* Clark.

BAYFIELDIA, sp. undet.
Pl. 55, figs. 20–23

Poorly preserved cranidia and pygidia of *Bayfieldia* are figured on account of their stratigraphic interest, being the only Cambrian fossils collected from the Grove limestone in place.

Glabella of the same shape as in the type species, with a trace of one pair of glabellar furrows. Frontal area not completely preserved, seemingly consisting of downsloping preglabellar field and elevated border as in *B. tumifrons*. Palpebral lobes about 1/3 the glabellar length, close to glabella, defined by a distinct but shallow palpebral furrow. Anterior facial sutures almost parallel. Posterior area not preserved.

Pygidium with prominent axis reaching the posterior margin, showing 2 rings and a terminal section. Pleural lobes downsloping, without border furrow, with three pairs of pleural furrows; margin extended into 4 pairs of strong spines.

As far as can be determined from the fragmentary material available, this form is essentially identical with the type species, described from boulders in the Levis conglomerate.

Occurrence.—Grove limestone, 30–50 feet above base of formation (loc. ccb/4), quarry near Ceresville, Frederick Co., Maryland.

Figured specimens.—USNM 136959.

Family SAUKIIDAE Ulrich & Resser, 1933

Genus PROSAUKIA Ulrich & Resser, 1933

PROSAUKIA STOSEI (Walcott)

Pl. 54, figs. 16–22

Saukia stosei WALCOTT, 1914, p. 384, pl. 69, figs. 3–5.

Prosaukia stosei (Walcott). WILSON, 1952, p. 316.

New material much better preserved than the types allows a supplementary description of the species.

Glabella parallel-sided in front of the fourth glabellar furrow, wider between this furrow and the occipital furrow, truncated in front. Fourth glabellar furrow continuous across the glabella, furrows of third pair meeting through a shallower median portion; furrows of second pair shallow, limited to the sides; first pair absent. Occipital furrow as deep as fourth glabellar furrow. Occipital ring wider (tr.) than last glabellar lobe, bearing a slender median spine of undetermined length. Palpebral area upsloping; palpebral lobe half as long as the glabella, defined by a well-impressed palpebral furrow; curvature of palpebral lobes increasing posteriorly; posterior end much farther from dorsal furrow than anterior end. Facial suture anterior to the palpebral lobe distant from dorsal furrow by about one-tenth of the glabellar width, thence directed in straight, somewhat divergent course to the sharp anterior cranidial angle. Frontal area divided into a flat preglabellar field and a convex border whose median width (sag.) almost equals the median length (sag.) of the preglabellar field. Posterior area very slender, parallel-sided; posterior border furrow deep proximally, becoming shallower distally and passing onto the free cheek before reaching the end of the posterior area.

Free cheek with moderately convex ocular platform and rather deep, wide border furrow. Lateral border furrow extending backward beyond its junction with the posterior border furrow; the latter broad and deep but becoming shallower before meeting the lateral furrow. Border convex, of uniform width. Genal spine somewhat shorter than the rest of the free cheek.

Pygidium with strongly prominent, tapered axis composed of 5 or 6 rings and a terminal section, extended into a postaxial ridge. Length of axis two-thirds of pygidial length. No axial nodes or spines. Pleural platforms strongly downsloping to slightly concave marginal area. Five or 6 pairs of pleural furrows and 4 pairs of interpleural grooves impressed; grooves narrower than the furrows, of the usual saukiid pattern, starting close to the succeeding furrow, diverging from it, then converging to and merging with it in the concave marginal area. Margin of doublure as usual marked by a slight impressed line on dorsal test, showing a doublure of average width somewhat over one-third of the pygidial length. Ratio of pygidial width to length 1.6.

Glabella and prominent parts of the fixed cheeks tuberculated; preglabellar field smooth; anterior border transversely striated. Ocular platforms tuberculated, the tubercles in the anterior portion being arranged to form irregular, longitudinal ridges; border of free cheeks striated. Large tubercles of cranidium and free cheeks visi-

ble also on internal surface. Rings of pygidial axis with smaller tubercles, arranged to form wrinkled longitudinal lines. Prominent portions of pleural platforms with similar wrinkled ornamentation; remaining pleural surface with low, wrinkled transverse terrace lines.

Length of largest cranidium collected 18 mm.

It is difficult to compare limestone material with the species from the upper Mississippi valley described by Ulrich and Resser and revised by Raasch (1952). Ulrich and Resser described 4 species in the group with tuberculated test and an occipital spine. Raasch considers one of these unidentifiable and the other 3 representing a single species, *P. beani*. The latter, as far as can be determined from poorly preserved impressions of cranidia (the only known part) is similar in general shape to the present form. *Prosaukia welleri* Resser from New Jersey, as illustrated by Howell (1945), differs from *P. stosei* in the reduced preglabellar field and straight-sided, conical glabella.

Occurrence.—The type locality is in the upper Conococheague formation near Scotland Junction, Pennsylvania. The specimens figured herein were collected from the Conococheague at localities cca and cca/3, Franklin County, Pennsylvania. Also occurring at locality ccn/2, Washington County, Maryland.

Types.—Syntypes: USNM 58673. Plesiotypes: USNM 136960–1.

PROSAUKIA CORRUGATA Rasetti, n. sp.
Pl. 54, figs. 4–14

Available material.—A few large cranidia, free cheeks, and several pygidia; also numerous parts of immature individuals.

Description.—Glabella slightly and regularly tapered, of moderate convexity, showing an exceedingly faint median keel on interior casts. Fourth glabellar furrow continuous; third pair shallow and not joining across the glabella; second pair shorter, very shallow in the interior cast and barely indicated on the outer surface by lack of ornamentation. Occipital furrow rather shallow; occipital ring with a slender, short spine preceded by a small node. Palpebral area almost horizontal; palpebral lobes more than half as long as the glabella, regularly curved. Anterior branch of facial suture immediately in front of the eyes distant from dorsal furrow rather more than one-tenth of the glabellar width. Anterior facial sutures divergent at about 30°, anterior angles of cranidium sharp. Preglabellar field somewhat shorter (sag.) than median width (sag.) of border. Posterior area slender, tapered, with border furrow passing onto the free cheek before reaching the distal end.

Free cheek showing a narrow, long, semicircular visual surface and a proportionately much shorter portion of the facial suture from the eye to the anterior border furrow than in *P. stosei*. Lateral border very prominent; posterior border less elevated.

Pygidium with prominent, tapered axis composed of 8–10 rings plus a terminal section, followed by a postaxial ridge. Axis occupying almost three-fourths of the pygidial length. Pleural platforms downsloping, but not as steeply as in *P. stosei*. Pleural furrows and interpleural grooves shallower and more nearly parallel to each other than in that species; six or seven pairs of furrows and grooves visible. Doublure about half as wide as the pygidial length.

Ornamentation of all prominent parts of cranidium, free cheek and pygidium consisting of fine, irregular, elevated lines, forming a vague concentric pattern on the glabella, approximately parallel to the outline of the eye on the ocular platform, parallel to the margin on the border of the cranidium and free cheek, approximately longitudinal on the pygidial axis, and parallel to the posterior margin on the pleural lobes. Exfoliated specimens appear smooth.

Length of largest cranidium (exclusive of occipital spine) 23 mm. Length of largest pygidium 16 mm., width 26 mm. Fragments indicate that the species may attain a larger size.

Ontogeny.—Well preserved, immature forms were found in a coquina composed exclusively of fragments of this species. Since immature Saukiidae do not seem to have been previously described, several specimens are illustrated and briefly discussed.

The smallest cranidium observed belongs to an early meraspid stage and has a length of 0.3 mm. It is not well preserved and its presence is mentioned to point out the small size of the early stages of such a large trilobite. The next, well preserved cranidium is 0.7 mm. long. The glabella is long, subcylindrical, slightly tapered in the posterior two-thirds but slightly enlarged in the anterior portion. In addition to the occipital furrow, the posterior glabellar furrow is impressed across the glabella, and two other pairs of shallow furrows are visible at the sides. The frontal area is a narrow (sag.), undifferentiated band. Anterior pits are well marked at the anterior angles of the glabella. A short, faint ocular ridge starts immediately behind the anterior pit and joins the long, narrow, poorly defined palpebral lobe. The latter has about two-thirds of the glabellar length. The posterior area is not well exposed, but seems to be relatively shorter (tr.) than in the adult.

There are several cranidia in the range 1.0–1.4 mm. At these stages, the glabella is more definitely straight-sided and slightly tapered over its entire length. The posterior pair of glabellar furrows is confined to the sides, and the other two pairs are short and very shallow. The occipital furrow is well impressed and the occipital ring is extended into a relatively broad but not very long spine. The anterior pits are very pronounced. The frontal area is relatively wider (sag.) than in the previous stage but still not differentiated into preglabellar field and border. The palpebral lobes remain long and narrow, the ocular ridges become indistinct, and the palpebral furrow is somewhat better impressed.

Cranidia 3–4 mm. long already show to a large extent the features of the adult in the shape of the glabella, character of glabellar furrows, division of the frontal area into preglabellar field and border, depth of palpebral furrow, and size and shape of palpebral lobes.

A transitory pygidium 0.6 mm. long is figured. Its axis is strongly tapered, and the ratio of width to length is greater than in the pygidia of later stages. Pygidia 4 mm. long have essentially the adult features, differing only in the proportionately longer axis and narrower doublure. These characters continue to change in the same direction even after the pygidium has attained a length of 10 mm. and should be kept in mind when comparing specimens of Saukiidae of different sizes.

Remarks.—This species belongs to the group characterized by Ulrich and Resser by lacking tuberculation and possessing an occipital spine. Close comparison with their species cannot be made owing to the poor preservation of sandstone material. In the upper Mississippi valley species of this group of *Prosaukia* occur in the Franconian and are therefore much older than the form under discussion.

Occurrence.—The holotype and all other figured specimens were collected from the upper Conococheague at locality cca/1, Franklin County, Pennsylvania. A coquina of fragments of this species was also found in presumably equivalent beds of the Conococheague (loc. cci/1) in the uppermost part of Wilson's section 45-lw (part I), SW of the track of the Winchester and Western Railroad, 1.6 miles SW of the center of Winchester, Virginia.

Types.—Holotype: USNM 136962. Paratypes: USNM 136693.

Family PTYCHASPIDIDAE Raymond, 1924

Genus KEITHIELLA Rasetti, 1944

Type species: *Arionellus cylindricus* Billings.

KEITHIELLA CYLINDRICA (Billings)

Pl. 51, fig. 23

Arionellus cylindricus BILLINGS, 1860, p. 314, fig. 14; in LOGAN, 1863, p. 237, fig. 264; 1865, p. 406, fig. 385.

Agraulos cylindricus (Billings). MILLER, 1889, p. 527, fig. 955.

Keithiella cylindrica (Billings). RASETTI, 1944, p. 243, pl. 39, figs. 39–41; 1945a, p. 469, pl. 61, fig. 8.

A single, poorly preserved cranidium agrees with the types in all observable features, in particular, the deep glabellar furrows and upsloping palpebral area that characterize the species.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Types.—Plesiotype: USNM 136964.

KEITHIELLA, sp. undet.
Pl. 52, figs. 17,18

A single cranidium, lacking the occipital ring but otherwise well preserved, differs from all described species of *Keithella* but does not warrant naming a new species.

Glabella straight-sided, slightly tapered, sharply truncated in front, defined laterally by a very deep and broad dorsal furrow. Three pairs of glabellar furrows visible, all short and not connected across the glabella. Palpebral area rising steeply; palpebral lobes small, elevated above the palpebral area. Anterior border furrow straight, shallow, confluent with dorsal furrow in front of glabella. Border wide, not steeply inclined. Anterior facial sutures divergent in front of eyes, anterior angles of cranidium widely rounded. Surface of test entirely covered with wrinkled raised lines. Length of cranidium, allowing for missing occipital ring, 6 mm.

This form has the deep dorsal furrow and upsloping palpebral area of *K. cylindrica*, but differs in the tapered glabella, lack of connecting posterior glabellar furrows, and different ornamentation.

Occurrence.—Conococheague formation (loc. ccn/2), Washington County, Maryland.

Figured specimen.—USNM 136989.

Genus KEITHIA Raymond, 1924

Type species: *Keithia schucherti* Raymond.

KEITHIA INTERMEDIA Rasetti, n. sp.
Pl. 54, figs. 23–27

Available material.—Several cranidia and pygidia moderately well preserved, mostly lacking the test.

Description.—Glabella long and narrow, slightly wider in the middle, moderately convex in both directions, not sharply truncated in front. Posterior glabellar furrows moderately deep, not connected across the glabella; third pair shorter and shallow; second pair barely visible. Occipital furrow impressed throughout; occipital ring short (sag.), bearing a small node. Frontal area downsloping; border furrow merging with dorsal furrow in front of glabella; border downsloping, wide (sag.) and flat. Palpebral area somewhat convex transversely, on the average horizontal, half as wide as the glabella; palpebral lobes one-eighth as long as the glabella. Anterior facial sutures convex outward, on the average convergent. Posterior branch directed outward and backward with moderate curvature to posterior margin; posterior area deeply furrowed.

Pygidium attributed to the species with strongly prominent axis composed of 3 rings and a terminal section, abruptly terminated, followed by a low postaxial ridge. Pleural lobes slightly downsloping, with 4 pleural furrows and 3 interpleural grooves; furrows and grooves form together broad depressions separated by narrow ridges. Border furrow wide and shallow, poorly defined; border slightly raised, very narrow. Posterior margin raised on midline. Ratio of width to length 1.8.

The cranidia are seemingly exfoliated and show no ornamentation. None appears on the pygidia either, although these appear to preserve the test. Length of largest cranidium 6.5 mm.

Remarks.—This form is another connecting link between *Keithia* and *Keithiella* (like a species described by the writer as *Keithiella brevis*). It resembles *Keithiella* in the elongate glabella which does not overhang the anterior border, but is like *Keithia* in having disconnected glabellar furrows and horizontal palpebral area. The closest species is probably *Keithia subclavata* (Billings), which has a pear-shaped, more convex, glabella and narrower anterior border. The pygidium closely resembles that of *Keithiella speciosa* (Walcott) as described by the author.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Types.—Holotype: USNM 136965. Paratypes: USNM 136966.

KEITHIA, sp. undet.
Pl. 51, fig. 24

One cranidium associated with the preceding species differs in several characters that bring it closer to *Keithia subclavata*. The glabella is proportionately shorter and wider than in *K. intermedia* but not strongly convex as in *K. subclavata*, while the border is narrow like in the latter species.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Figured specimen.—USNM 136967.

Genus EUPTYCHASPIS Ulrich, 1931

Type species: *Euptychaspis typicalis* Ulrich.

EUPTYCHASPIS TYPICALIS Ulrich

Pl. 52, figs. 11–13

Euptychaspis typicalis ULRICH, in BRIDGE, 1930, p. 218, pl. 19, figs. 5–7.

Several cranidia of *Euptychaspis* do not differ in any significant feature from the types of the species.

Occurrence.—Conococheague formation (loc. ccn/2), Washington County, Maryland.

Types.—Plesiotypes: USNM 136968–9.

Family ?SHUMARDIIDAE Lake

Genus IDIOMESUS Raymond, 1924

Type species: *Idiomesus tantillus* Raymond.

IDIOMESUS INTERMEDIUS Rasetti, n. sp.

Pl. 51, figs. 25,26

Available material.—A few cranidia.

Description.—This form is so similar to the type species that a complete description seems unnecessary. The general shape of the cranidium and its various parts are the same as in *I. tantillus*, except that, in addition to the posterior transglabellar furrow, there is another pair of furrows in form of well-marked pits adjacent to the dorsal furrow. Another species, *I. levisensis* (Rasetti) has two similar pairs of pits, hence the present form is intermediate between them. The largest (holotype) cranidium is 4 mm. long.

Occurrence.—Conococheague limestone; type locality ccn/2, Washington County, Maryland; also at locality cca, Franklin County, Pennsylvania.

Types.—Holotype: USNM 136970. Paratypes: USNM 136971–2.

Family ENTOMASPIDIDAE Ulrich, 1930

Genus ENTOMASPIS Ulrich, 1930

Type species: *Entomaspis radiatus* Ulrich.

ENTOMASPIS RADIATUS Ulrich

Pl. 52, figs. 9,10

Entomaspis radiatus ULRICH, in BRIDGE, 1930, p. 213, pl. 19, figs. 14–16.

Entomaspis radiatus Ulrich. RASETTI, 1952b, p. 798, pl. 117, figs. 1–11, text-figs. 1–3.

A single, well-preserved pygidium agreeing in all respects with the pygidia from the type locality was collected from the upper Conococheague at the Scotland locality. Another, poorly preserved pygidium collected from a loose block of Frederick limestone may tentatively be assigned to the species. These are the first reported occurrences of the genus in the Appalachian province.

Occurrence.—Conococheague formation (loc. cca), Franklin County, Pennsylvania; also in loose block of Frederick limestone (loc. ccm/1) in the suburbs of Frederick, Maryland.

Types.—Plesiotypes: USNM 136973–4.

Family ?ODONTOPLEURIDAE Burmeister, 1843

Genus undetermined

"ACIDASPIS" ULRICHI Bassler

Pl. 51, fig. 27

Acidaspis ulrichi BASSLER, 1919, p. 355, pl. 37, figs. 6–8.

Bassler described and figured a peculiar, spinose free cheek collected from loose slabs of Frederick limestone and attributed to an odontopleurid. At that time the formation was believed to be Middle Ordovician and there was no reason to question the family assignment. When the Frederick limestone was found to be Upper Cambrian, the systematic position of this trilobite became doubtful. Similar free cheeks are known from the Upper Cambrian of Nevada, where they occur in association with *Eurekia*, and the writer collected one specimen from the Gorge formation of Vermont. Kindle and Whittington (1958) mention the occurrence of this fossil in western Newfoundland.

Since Lermontova (1951) and Tschernysheva (1953) have shown the presence of seemingly authentic Odontopleuridae in the Middle and Upper Cambrian of Siberia, the occurrence of a member of the family in the Upper Cambrian of North America no longer appears implausible. However, a final decision on the systematic position of the species must await the discovery of other portions of the exoskeleton, especially the

cranidium. One feature of the free cheeks is in disagreement with what is known of all the post-Cambrian Odontopleuridae. These have the free cheeks separated from the rostrum by paired connective sutures. In "*Acidaspis*" *ulrichi*, the free cheeks seemingly consisted of a single piece, since specimens are known (such as the one figured herein) where the free cheeks, although dismembered from the cranidium, were preserved as a unit.

Occurrence.—Frederick limestone; loose slabs at locality ccm/1, in the suburbs of Frederick, Maryland.

Types.—Plesiotype figured herein (collected by A. P. Loeblich): USNM 136975.

Family undetermined

Genus LEVISELLA Ulrich, in Rasetti, 1944

Type species: *Dikelocephalus oweni* Billings.

LEVISELLA NASUTA Rasetti, n. sp.

Pl. 54, figs. 1–3

Available material.—Several cranidia, free cheeks, and pygidia moderately well preserved.

Description.—Glabella about as wide as long, subquadrate, slightly tapered in the anterior portion, moderately convex, unfurrowed. Occipital furrow well impressed throughout; occipital ring short (sag.). Dorsal furrow shallow. Palpebral lobes broken off in all available cranidia, but clearly close to the glabella as typical of the genus. Preglabellar field moderately long (sag.); anterior border furrow shallow, but marked by a series of very distinct puncta. Border wide (sag.), slightly convex, tapering at the sides, wider (sag.) medially than the preglabellar field. Posterior area very slender, parallel-sided. Anterior facial sutures diverging at an angle of about 45°. Surface apparently smooth.

Pygidium over twice wider than long. Axis very prominent, slightly tapered, with three rings and a terminal section, extended into a postaxial ridge. Pleural lobes with little relief, with three pairs of broad, shallow furrows terminating in the slightly concave, smooth border. Length of largest cranidium 10 mm., of largest pygidium 8 mm.

Remarks.—This form is obviously very close to *L. oweni* (Billings), from which it differs chiefly in the proportionately shorter and wider glabella, lack of glabellar furrows, and shorter preglabellar field. The shape of the glabella and the somewhat nasute extension of the anterior border on the midline distinguish it also from *L. brevifrons* Rasetti and *L. affinis* (Billings). The pygidia of all these species are practically indistinguishable.

Occurrence.—Loose block of Grove limestone (loc. ccb/2) in the suburbs of Frederick, Maryland.

Types.—Holotype: USNM 136976. Paratypes: USNM 136977.

Genus LOGANELLUS Devine, 1863

Type species: *Olenus ? logani* Devine.

LOGANELLUS CF. L. SIMILIS Rasetti

Pl. 51, figs. 28,29

Loganellus similis RASETTI, 1944, p. 247, pl. 38, figs. 21–23.

A cranidium and a pygidium from the Frederick limestone do not differ significantly from the types of the species. However, imperfect preservation and the meagre material do not allow a positive identification.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Figured specimens.—USNM 136978.

Genus ONCHONOTUS Raymond, 1924

Type species: *Menocephalus globosus* Billings.

ONCHONOTUS RICHARDSONI (Walcott)

Pl. 51, figs. 5,6

Levisia richardsoni WALCOTT, 1911, p. 86, pl. 17, figs. 4,4a.

Onchonotus richardsoni (Walcott). RAYMOND, 1924, p. 406.

Onchonotus richardsoni (Walcott). RASETTI, 1944, p. 249, pl. 38, figs. 31–34.

Several imperfect cranidia agree in all observable features with specimens from the type locality, the boulders in the Levis conglomerate, at Levis, Quebec.

Occurrence.—Loose block of Grove limestone (loc. ccb/2) in the suburbs of Frederick, Maryland.

Types.—Plesiotypes: USNM 136979.

Genus APOSOLENOPLEURA Raymond, 1937

Type species: *Aposolenopleura dunbari* Raymond.

APOSOLENOPLEURA PLICATA Rasetti, n. sp.
Pl. 51, figs. 19–22

Available material.—Two exfoliated, fairly well preserved cranidia.

Description.—Glabella slightly tapered, subtruncated in front, strongly elevated, defined by a wide, deep dorsal furrow. Glabellar furrows short and shallow. Occipital furrow wide and deep, occipital ring simple. Frontal area downsloping; preglabellar field consisting medially of a broad depression formed by the confluence of the dorsal and border furrows. Border elevated, convex, strongly arched transversely when viewed from the front. Palpebral area very narrow, sloping up from the dorsal furrow and then down to the palpebral lobe, forming a rounded ridge between the palpebral lobe and the glabella; palpebral lobe about one-quarter as long as the glabella. Anterior facial sutures slightly divergent; posterior branch curving to posterior margin after a long, straight transverse course. Posterior area deeply and broadly furrowed. Length of larger cranidium 4 mm.

Remarks.—This species is fully typical of the genus, differing from *A. dunbari* chiefly in the shape of the palpebral area. The genus is known for the Gorge formation and the Levis boulders.

Occurrence.—Frederick limestone (loc. ccb/3), road cut in the suburbs of Frederick, Maryland.

Types.—Holotype: USNM 136980. Paratype: USNM 136981.

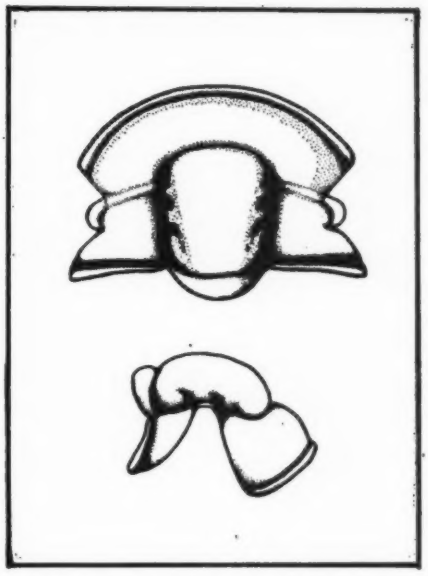
Genus BOWMANIA Walcott, 1924

Type species: *Arethusina americana* Walcott.

BOWMANIA PENNSYLVANICA Rasetti, n. sp.
Pl. 55, figs. 1–5; text-fig. 1

Available material.—Several cranidia.

Description.—Cranidium with the separate parts highly convex. Glabella parallel-sided, strongly convex in both directions, defined by a dorsal furrow that is very deep and wide laterally but shallower anteriorly. Three pairs of glabellar furrows, pit-like, confluent with the dorsal furrow; the posterior pair deep, curving backward, the next pair shorter, the anteriormost pair barely indicated. Occipital furrow well impressed throughout, deeper at the sides, occipital ring somewhat expanded medially. Preglabellar field half as long as the glabella, longitudinally convex; border furrow sharp and narrow, border narrow, of even width, convex. Palpebral area about half as wide as the glabella, convex, rising above the dorsal furrow but not attaining the height of the glabella; ocular ridges strongly marked, oblique, straight; palpebral lobes about one-fourth as long as the glabella, moderately elevated, set off by a shallow palpebral furrow, situated somewhat back of the level of the glabellar midpoint. Posterior border furrow deep. Anterior facial sutures appearing strongly divergent in dorsal view, directed steeply downward. Posterior branch directed outward, backward and downward from the palpebral lobe, reaching the posterior margin without much curvature. All parts of cranidium very finely granulated with, in addition, numerous coarse tubercles. Length of largest cranidium 5 mm.



TEXT-FIG. 1—*Bowmania pennsylvanica* Rasetti, n. sp. Dorsal and lateral views of cranidium, ×5.

Remarks.—The finding of this species

marks the first definite occurrence of *Bowmania* in the Appalachians, since a species from New Jersey, *Anomocare parvula* Weller, is too poorly represented to make the assignment to *Bowmania* convincing (Howell, 1945).

The present species differs from *B. americana* chiefly in the glabella proportionately wider at the anterior end, shorter frontal area, greater convexity of the separate cranidial parts, and coarser ornamentation.

Occurrence.—Conococheague formation (loc. cca), Franklin County, Pennsylvania. Two poorly preserved cranidia tentatively attributed to the species were collected from a loose block of Frederick limestone (loc. ccm/1) in the suburbs of Frederick, Maryland.

Types.—Holotype: USNM 136982. Paratypes: USNM 136983.

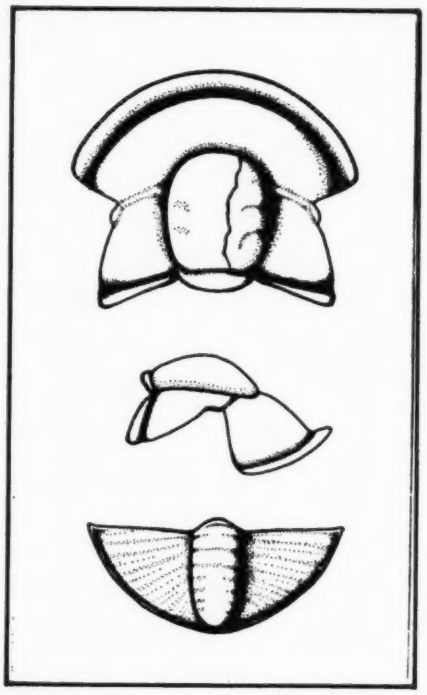
Genus CONOCOCHEAGUEA Rasetti, n. gen.

Description.—Small trilobites with highly convex cephalon. Glabella subovate, rising above the cheeks, occupying half the cranidial length, with traces of glabellar furrows; occipital furrow impressed, occipital ring short (sag.) and simple. Preglabellar field convex, downsloping; anterior border furrow and border well developed; palpebral area downsloping, about half as wide as the glabella. Palpebral lobes very small, at level of glabellar midpoint. Ocular ridges distinct. Anterior facial sutures directed outward and downward; posterior branch almost straight outward and backward to posterior margin; posterior border furrow well impressed. Pygidium attributed to the genus wide and short; anterior outline straight, posterior margin rather regularly curved; anterior angles sharp. Axis prominent, cylindrical, occupying whole length of pygidium, of many poorly defined segments. Pleural lobes horizontal, with traces of segmentation; border slightly raised.

Type species.—*Conococheaguea ovata* Rasetti, n. sp.

Geographic and stratigraphic range.—Trempealeauian of the central Appalachians.

Remarks.—The writer is at a loss trying to find a known trilobite genus with which the present form might be compared. The strong divergence of the anterior facial sutures, causing the cranidium to be somewhat wider between the anterior angles than between the tips of the posterior areas, gives this trilobite an unusual aspect. The pygidium is unusual for Cambrian trilobites, suggesting such Ordovician forms as the Raphiophoridae or the Trinucleidae. For the present the affinities of the genus remain obscure.



TEXT-FIG. 2.—*Conococheaguea ovata* Rasetti, n. gen., n. sp. Dorsal and lateral views of cranidium, pygidium, ×5.

CONOCOCHEAGUEA OVATA Rasetti, n. sp.
Pl. 52, figs. 19–26; text-fig. 2

Available material.—Known from several scores of cranidia and a few pygidia, well preserved in limestone.

Description.—Features mentioned in the generic diagnosis are omitted. Glabella well rounded in front, subovate in adult individuals but somewhat more straight-sided in the smaller cranidia. Glabellar furrows obsolete on outer surface; on the interior

cast, two faint pairs of furrows and a suggestion of a third are visible on whitened specimens. The furrows are narrow, start from the dorsal furrow, and curve regularly inward and backward. Preglabellar field sloping down steeply to wide border furrow; border of uniform, moderate width, slightly convex. Anterior angles of cranidium narrowly rounded by facial sutures. Ocular ridges better visible on internal casts, narrow, almost straight, directed outward and backward; palpebral lobes inconspicuous, slightly elevated, about 1/6 the glabellar length. Surface of cranidium with scattered fairly large granules, visible both on the outer surface and on casts of the interior; in the latter case there is also a suggestion of longitudinal, irregular lines of the preglabellar field. Pygidium 2.4 times wider than long. Axis showing very faintly 7 rings plus a terminal section; pleural furrows straight, extending to border but extremely faint. Length of largest cranidium 6 mm. Length of largest pygidium 2.2 mm., width 5.3 mm.

Remarks.—The few pygidia were found closely associated with the cranidia at both localities, suggesting the present assignment. Furthermore, there is no other cranidium to which they could be plausibly attributed.

Occurrence.—Conococheague limestone. The type locality is cca, Franklin County, Pennsylvania. Also locality U.S.G.S. 2186, 0.5 mile north of the preceding, and locality ccn/2, Washington County, Maryland.

Types.—Holotype: USNM 136984. Paratypes: USNM 136985–7.

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EXPLANATION OF PLATE 55

FIGS. *1–5*—*Bowmania pennsylvanica* Rasetti, n. sp., ×5. *1–3*, Dorsal, frontal, and lateral views of cranidium (USNM 136982, holotype); *4,5*, Cranidia (USNM 136983, paratypes). Conococheague limestone, loc. cca.

6–13—*Triarthropsis nitida* Ulrich. *6,7*, Lateral and dorsal views of pygidium, ×8; *8*, Pygidium, ×5; *9*, Free cheek, ×5; *10*, Lateral and dorsal views of cranidium, ×5; *12,13*, Cranidia, ×5 (USNM 136933, plesiotypes). Conococheague limestone, loc. cca.

14—*Richardsonella megalops* (Billings). Largely exfoliated cranidium, ×3 (USNM 136950, plesiotype). Grove limestone, loc. ccb/2.

15–18—*Richardsonella subcristata* Rasetti, n. sp. *15*, Cranidium preserving part of test, ×5 (USNM 136951, holotype); *16,17*, Dorsal and anterior views of exfoliated cranidium ×3; *18*, Pygidium with broken marginal spines, ×3 (USNM 136952, paratypes). Grove limestone, loc. ccb/2.

19—*Richardsonella* cf. *R. unisulcata* Rasetti. Exfoliated cranidium, ×5 (USNM 136953). Frederick limestone, loc. ccb/3.

20–23—*Bayfieldia*, sp. undet. *20*, Portion of exfoliated pygidium, ×3; *21*, Exfoliated cranidium, ×4; *22,23*, Dorsal and lateral views of exfoliated cranidium, ×2 (USNM 136959). Grove limestone, loc. ccb/4.

24–28—*Apatokephaloides macrops* Rasetti, n. sp. *24,25*, Dorsal and lateral views of exfoliated cranidium, ×5 (USNM 136956, holotype); *26*, Cranidium, ×5; *27,28*, Lateral and dorsal views of exfoliated pygidium tentatively attributed to the species, ×5 (USNM 136957, paratypes). Frederick limestone, loc. ccb/3.

29–32—*Apatokephaloides minor* Rasetti, n. sp. *29*, Cranidium, ×5 (USNM 136954, holotype); 30–32, Cranidia, ×5 (USNM 136955, paratypes). Grove limestone, loc. ccb/2.

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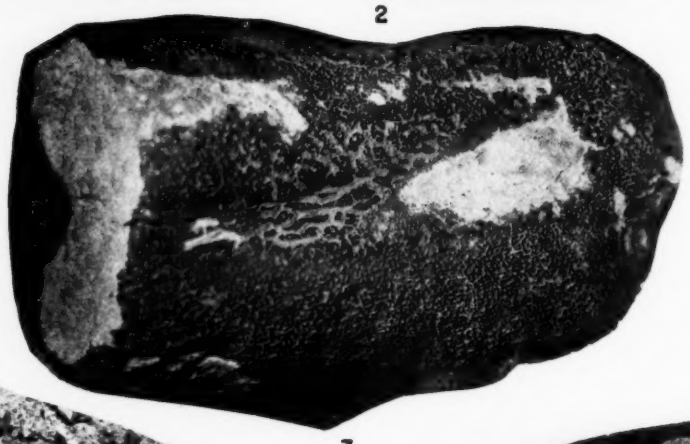

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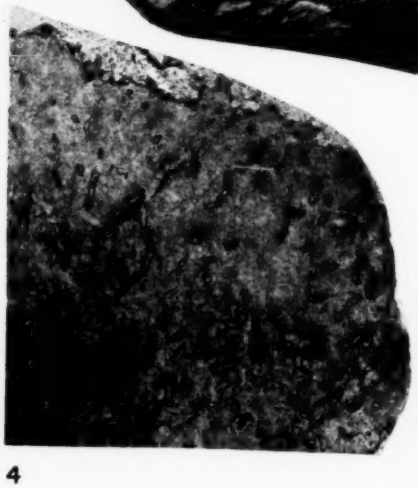

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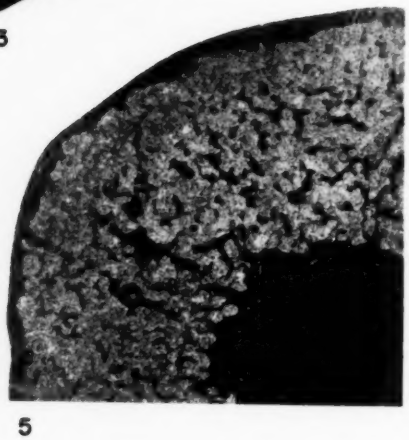

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JOURNAL OF PALEONTOLOGY, V. 33, NO. 3, P. 399–403, PL. 56, 1 TEXT-FIG., MAY 1959

SOME MISSISSIPPIAN AND PENNSYLVANIAN SPONGES FROM UTAH

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Department of Geology, Brigham Young University, Provo, Utah

ABSTRACT—The two previously described species of *Wewokella* and *Talpaspongia clavata* King occur in the uppermost Mississippian part of the Manning Canyon Formation in the Oquirrh Mountains, which is the earliest occurrence known to date. *Annulispongia interrupta*, a new dictyid form of the Titusvilliidae, occurs in the lowermost Pennsylvanian part of the same formation in the same area. *Talpaspongia* and *Annulispongia* occur consistently in limestone and *Wewokella* occurs in shale, suggesting a relationship of shallow cloaca in a turbid environment.

INTRODUCTION

FOUR species of fossil sponges have been collected from the uppermost Mississippian and lowermost Pennsylvanian rocks in the Oquirrh Mountains, in central Utah. Except for a new titusvillid form, these sponges have been described by King (1943) and Girty (1915) from Pennsylvanian and Permian rocks of the mid-continent. The Utah forms described here were all collected from the Manning Canyon Shale, defined by Gilluly (1932, p. 32–33) in the Oquirrh Mountains.

The Manning Canyon Shale consists predominantly of shale with minor interbeds of lithographic and fossiliferous limestone and quartzite. The formation includes rocks of youngest Chesterian and oldest Springeran ages. The boundary between the two occurs near the base of a prominent limestone unit approximately 480 feet above the base of the formation. With the exception of *Annulispongia*, the various specimens described here were collected from limestone and shale immediately below this marker unit.

Characteristically, *Wewokella* occurs in calcareous shale and very argillaceous limestone. In West Canyon (fig. 1) the sponges occur in a very dark greenish gray and black calcareous shale which contains a few nodules or concretions of black siltstone. Most of the specimens are iron-stained and the canal system filled with debris and silicified.

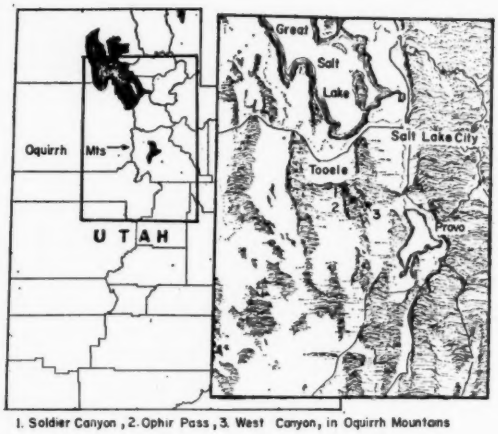
Specimens of *Talpaspongia* consistently occur in dark gray, very finely crystalline, medium- to thick-bedded limestone. Argillaceous content is low in the fossiliferous horizon, but shale beds occur immediately below and above. Branchiopods, crinoids, bryozoans, and corals are associated with the sponges at all localities collected.

EXPLANATION OF PLATE 56

FIGS. *1,2*—*Annulispongia interrupta*, n. sp. *1*, polished transverse section of holotype showing spicule character and arrangement of canals, ×2. *2*, side view of holotype specimen showing cup-shaped individuals of colony in various levels of weathering, ×1, locality 11029.

3,4, *Wewokella solida* Girty. *3*, side view of partially etched specimen showing prosochetes as small irregular sharp points, and apochetes as larger anastomosing structures in center of specimen. ×1, locality 11005. *4*, photomicrograph of transverse section showing apochetes in dark center and small prosochetes radiating through coarse spicular sponge wall, ×5, locality 11005.

5, *Talpaspongia clavata* King. Photomicrograph of thin section showing canal system in relation to coarse spicular sponge wall and central cloaca. Cloaca and canals now filled with detritus and appear dark. ×5, locality 11005.



TEXT-FIG. *1*.—Fossil sponge location.

Annulispongia occurs above the other fossils, approximately 800 feet above the base of the formation, and is known from a single specimen collected in Ophir Pass (locality 11029). It is in a limestone matrix with a lithology much like beds which bear *Talpaspongia*.

The most fossiliferous locality is exposed in West Canyon, on the eastern side of the Oquirrh Range (localities 11005, 11025). Both species of *Wewokella* and most specimens of *Talpaspongia* were collected here. Other specimens of both genera were collected, however, in Soldier Canyon, the type section of the Manning Canyon Shale, and at Ophir Pass, at the head of the South Fork of Soldier Canyon on the western side of the range. Specimens from West Canyon are consistently better preserved than those of the other localities.

SYSTEMATIC DESCRIPTIONS

Class HYALOSPONGEA Vosmaer, 1886
Order HETERACTINIDA Hinde, 1888
Family ASTERACTINELLIDAE
de Laubenfels, 1955
Genus WEWOKELLA Girty, 1911
WEWOKELLA SOLIDA Girty
Pl. 56, figs. 3,4

Wewokella solida GIRTY, 1911, N. Y. Acad. Sci. Annals, vol. 21, p. 121: GIRTY, 1915, U. S. Geol. Survey Bull. 544, p. 17, 18, pl. 1, figs. 12–13b.

Description.—Sponge body irregularly cylindrical, frequently slightly curved. Specimens at hand vary from 2.3 to 5.9 cm. in diameter and up to 12 cm. long. Complete specimens were not found, for both ends have been broken in all specimens. In two specimens a shallow cloaca approximately one-half as wide as the diameter, is preserved. Cloaca is developed only in terminal parts of the sponge, with prominent apochetes in the central part. Individual apochetes range from 0.9 to 1.1 mm. in diameter and anastomose irregularly in central part of sponge, rarely extending to within one third the diameter of the outside. Prominent prosochetes developed with roughly radial pattern. Most are from 0.25 to 0.4 mm. in diameter, piercing the entire body wall and emptying into the apochetes. In the specimens at hand, the canal wall is approximately 0.1 mm. thick and has been silicified. Although the prosochetes are generally radially disposed, they appear somewhat root-like when etched free of spicular material. Apochetes become more numerous toward the cloaca in observed specimens, increasing from 4 or 5 near the base to as many as 20 near the base of the cloaca.

Spicule structure, although preserved, is difficult to isolate. Where observed, spicules appear to be sphaerasters, typical of the family. Central masses of the spicules are from 1.0 to 1.5 mm. in diameter, and radiating rays considerably smaller but up to 1 mm. long. Dermal spicules or tissue is not preserved in the specimens at hand, even though many of the specimens are encrusted with cyclostome bryozoans.

Utah specimens agree well with the type descriptions of Girty (1911, 1915).

Occurrence.—Approximately 30 specimens were collected from the lower (Mississippian) part of the Manning Canyon Shale in the Oquirrh Range, Utah and Tooele Counties, Utah. Most specimens came from deeply weathered shale immediately below the "medial" limestone of the formation (Gilluly, 1932, p. 32–33) in both West Canyon (loc. 11005) and Soldier Canyon (11019). A single specimen of the species was also collected in the head of Chandler Fork of Ophir Canyon at Ophir Pass at approximately the same stratigraphic level (loc. 11022).

Stratigraphic occurrence of the sponges was so consistent (Moyle, 1958) that the

unit was used as a marker horizon for correlation. Specimens were collected from Soldier Canyon and Ophir Pass by Moyle, and from West Canyon by the writers and H. J. Bissell.

WEWOKELLA CONTORTA King, 1943

Wewokella contorta KING, 1943, State Geol. Survey Kansas Bull. 47, pt. 1, p. 27,28, pl. 2, figs. 1,8; pl. 3, fig. 5.

Discussion.—Five specimens which may be included in this species were collected from the Mississippian part of the Manning Canyon Shale. Specimens range in diameter from 32 to 61 mm. and up to 10 cm. long. All specimens are fragmentary with both ends broken. Forms considered of this species are associated in outcrops with *Wewokella solida* Girty and are similar to those specimens in nearly all respects. The primary difference is only that of growth form, *W. contorta* bending abruptly in its direction of growth and *W. solida* being relatively straight.

Occurrence.—All specimens included in this species collected during the present investigation, occur in the lower part of the Manning Canyon Shale. Most specimens were collected from West Canyon on the southeast side of the Oquirrh Mountains. Specimens occur in localities 11005, 11022.

Genus TALPASPONGIA King, 1943
TALPASPONGIA CLAVATA King, 1943
Pl. 56, fig. 5

Talpaspongia clavata KING, 1943, State Geol. Survey Kansas Bull. 47, pt. 1, p. 29,30, pl. 1, fig. 6; pl. 2, figs. 1,8.

Discussion.—Several large specimens, up to 7 cm. in diameter, have been collected from uppermost Mississippian rocks from the Manning Canyon Shale in the Oquirrh Range of central Utah. Specimens agree well with descriptions of the types by King (1943) and in addition show more vividly the differences between the canal systems of this genus and the closely related *Wewokella*. This difference can be readily seen in thin sections (figs. 4,5, Pl. 56). In *Wewokella* the canals have a relatively radial and constant space relationship, even though somewhat tortuous. More irregularly sized and spaced canals are developed in *Talpaspongia*. The main differences between the genera are still those pointed out by King in his original description (1943, pp. 29, 30) of the genus, but even fragments can be identified with fair certainty in thin sections.

Occurrence.—All specimens found in the present search occur in the Manning Canyon Shale in Soldier Canyon, the type section of the formation, in West Canyon, and in Ophir Pass (localities 11019, 11005, 11022).

Order LYSSAKIDA Zittel, 1877
Family TITUSVILLIIDAE Caster, 1943
Genus ANNULISPONGIA nov.

This new genus includes colonial sponges which appear similar to fragments of *Titusvillia* in general growth form, but which are larger and with only two well differentiated layers within the sponge wall. The layer lining the cloaca and the upper part of the buds is more dense than the remainder of the cups. It is unknown whether this genus branched as do genera already included within the family Titusvilliidae, because of the fragmentary nature of the single specimen found. The genus is included in the Titusvilliidae largely because of the compound cup-shape of the colony and because of the general dictyid character of the body spicules.

Genotype.—*Annulispongia interrupta* n. sp.

ANNULISPONGIA INTERRUPTA n. sp.
Pl. 56, figs. 1,2

Diagnosis.—Compound linear budded, cup-shaped dictyid sponge appearing superficially like *Titusvillia*, but walls composed of two spicular layers and pierced by numerous prosochetes and apochetes.

Description.—The holotype, and only specimen, consists of a partially weathered linear budded colony 7 cm. long and 3.1 cm. wide at maximum expansion of the cups, composed of 7 buds, each from 1.2 to 1.5 mm. long. Center pierced by continuous cloaca throughout, approximately one-third as wide as maximum diameter, but now obloid because of lateral flattening of the specimen.

Individual cups shaped like flattened inverted cones, 18 to 20 mm. in diameter at the base, expanding slowly in lower half,

then rapidly in upper half to a maximum diameter of 29 to 31 mm. Upper surface of cup diverges from axis approximately 60 or 70 degrees and is a relatively smooth, evenly sloping conical surface. Margins of the cups are poorly preserved but were probably distinctly keeled. Marginal spicule tufts such as those inferred for *Titusvillia* were not observed in the specimen.

In transverse section the two distinct spicular layers can be differentiated, the inner is most dense and 1.5 to 3.0 mm. thick in sections observed, the outer is composed of relatively widely, but evenly spaced spicules. The outer layer is 3.0 to 4.5 mm. thick where observed, approximately midway up the last cup preserved in the fragment.

Apochetes appear horizontal or inclined downward toward the center of the sponge, leading to the cloaca and roughly parallel with the upper surface of the cup. They range from 0.3 to 0.4 mm. in diameter and some extend nearly completely through the sponge wall. Prosochetes lie nearly normal to these, particularly in the upper parts of the cups. Prosochetes generally parallel the outer surface of the lower part of the cup and occur in both a horizontal and vertical position, leading to the larger apochetes. Where observed in side view and in transverse section, prosochetes range in diameter from 0.1 to 0.2 mm., the larger size being nearer the apochetes. Apochetes occur in a space grid every 1 to 1.5 mm., but prosochetes closely packed, occurring 3 or 4 in the same space.

Spicules of the outside body wall are relatively symmetrical hexacts. In lateral areas the horizontal rays become more pronounced and form the concentric layers seen in transverse section. Within the body wall the vertical rays may become elongate producing the vertical texture observed along the weathered surface of the specimen. In general spicule rays are from 0.03 to 0.04 mm. in diameter and individual rays from 0.1 to 0.2 mm. long. Some rare rays approach 0.5 mm. long. There seems to be a slight expansion of the rays near their common junction at the center of the spicule.

Spicules which form the inner part of the body wall are slightly more irregular as judged from transverse section. They are also thicker and more closely spaced, producing a network distinctly finer than that of the main body wall.

Occurrence.—The single specimen of the species was collected from the upper part of the Manning Canyon shale, 800 feet above the base of the formation, in lowermost Pennsylvanian rocks. The locality is at the northeast end of Ophir Pass, in the northeastern corner of Sec. 11 (unsurveyed), T. 5 S., R. 4 W., Tooele County, Utah.

Discussion.—Since the genus *Annulispongia* is at the present monotypic, there can be no differentiation between generic and specific structures. The distinctive characters of the form have been mentioned above and these serve to differentiate if from the smaller related forms of the Titusvilliidae.

This is the first sponge of this family recognized in the Pennsylvanian system, and it helps in outlining some trends of evolution within the group. A canal system, inferred by Caster in *Titusvillia* (1939, 1941), is well developed in *Annulispongia*. The three-layered wall which characterizes other members of the family (Caster, 1939, p. 1) has developed into a two-layered one. The inner layer, only poorly defined in *Titusvillia* (Caster, 1939, fig. 2b) is well differentiated in *Annulispongia*, but the reverse is true of the outer wall, which is thick in early members of the family and nearly gone in *Annulispongia*.

It is unfortunate that only a single fragment of the colony of *Annulispongia* has been found, for little can be done to determine whether the genus was branched, or if so, the manner of branching.

Type.—The holotype, the only specimen, is in the collections at the Department of Geology, Brigham Young University. Specimen number 11029–1.

LOCALITY DESCRIPTIONS

Locality 11005: 150 yards N 20°W of first intersection of major gully from southwest with Iron Canyon, approximately 1 mile west of junction with main West Canyon. In small gully at base of small hill at west end of sage flat in shale and fossil "hashy" limestone. Sec. 3, T. 5 S., R. 3 W., Tooele County, Utah

Locality 11006: In limestone ledge at crest of hill due north of intersection of third gully from southwest with Iron Canyon, 1¼ mile west of

Iron Canyon-West Canyon junction. Sec. 3, T. 5 S., R. 3 W., Tooele County, Utah.

Locality 11019: East side mouth of major gully from north, 300 yards east of mine dumps on north side of road near mouth of Soldier Canyon in argillaceous limestone near the valley floor. Sec. 33, T. 5 S., R. 4 W., Tooele County, Utah.

Locality 11022: In argillaceous limestone near center of Ophir Pass between South Fork of Soldier Canyon and Chandler Fork of Ophir Canyon in barren area between aspen trees north of cabin at pass. Sec. 11, T. 6 S., R. 4 W., Tooele County, Utah

Locality 11025: Approximately same as locality 11005, but in limestone and shale near top of hill, a few hundred feet northwest, in gully and along northeast slope, Sec. 3, T. 5 S., R. 3 W., Tooele County, Utah.

Locality 11029: In same pass as 11022 between Soldier Canyon and Ophir Canyon, but near east side of pass, 800 feet above base of Manning Canyon shale near Oquirrh limestone outcrops, Sec. 11, T. 6 S., R. 4 W., Tooele County, Utah.

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JOURNAL OF PALEONTOLOGY, V. 33, NO. 3, P. 404–427, PLS. 57–60, 1 TEXT-FIG., MAY 1959

A *PTYCHASPIS* FAUNULE FROM THE BEAR RIVER RANGE, SOUTHEASTERN IDAHO

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ABSTRACT—Faunules of the *Ptychaspis* subzone of the Franconian stage appear to be widespread in southeastern Idaho and eastern Utah, but have not previously been described. The trilobite coquina limestone furnishing this collection is from the St. Charles limestone, 250 feet to 273 feet above the top of the Worm Creek quartzite member, on the ridge north of Mink Creek, Idaho. Ten genera and 14 species of trilobites, two genera and species of gastropods, three genera of brachiopods, *Hyolithes*, sponge spicules and cystoid fragments comprise the assemblage. The new species, *Ptychaspis bullasa*, *Idahoia* (*Meeria*) *modesta*, *Saratogia fria*, *Bellaspis? oblonga*, *Taenicephalina globula*, *Anconochilus idahoensis*, and the new genus *Minkella americana*, are described. In the population of the latter species probable male and female forms are indicated.

The faunule is placed at or near the top of the *Ptychaspis granulosa* teilzone. The appearance of *Taenicephalina*, *Bellaspis*, *Minkella*, a member of the Dokimocephalidae, and two species of *Pseudagnostus* occurring also in eastern Nevada shows the first interminglings of far western or extracratonic faunal elements with a characteristic shallow shelf assemblage, a phenomenon fully compatible with the geographic position of the collection.

INTRODUCTION

IN 1954 while examining some Cambrian fossils obtained by Allen Keller from the Bear River Range, the senior author noted one collection from the St. Charles limestone which was a coquina of *Ptychaspis* cranidia. This was the first observation of the genus *Ptychaspis* this far west in the Cordilleran region. Additional material promised to supplement significantly the limited knowledge of the *Ptychaspis-Prosaukia* assemblages in this area.

The *Ptychaspis-Prosaukia* faunizone assemblages were first recognized in and have been most completely described from the Minnesota-Wisconsin areas of the upper Mississippi valley (Hall, 1863; Nelson, 1951; Bell, Feniak & Kurz, 1952). Genera characteristic of these faunules have been described or listed from central Montana (Lochman, 1950), Lincoln County, Wyoming (Schultz, 1914) and the northern Wasatch Mountains (Walcott, 1925; Resser, 1942). Recently several assemblages of the zone have been described from southwestern Montana (R.V. Grant, unpublished thesis, 1957).

In the fall of 1957 Robert Bright collected additional material from the Keller locality and furnished detailed information on the stratigraphic position of the collection. Mr. Bright has just completed mapping in the central Bear River Range and reports that faunules of the *Ptychaspis-Prosaukia* faunizone are abundant and widespread in the St. Charles formation of southeastern Idaho.

ACKNOWLEDGMENTS

The authors wish to thank Dr. W. Lee Stokes for making available Allen Keller's collection, and Mr. Robert Bright for his invaluable assistance in furnishing the larger supplementary collection and information on the stratigraphy of the faunule. The completion of the study was made possible by a Research Assistantship Grant to the junior author from the New Mexico Institute of Mining and Technology.

HORIZON AND LOCALITY

The collection was obtained from thin limestone beds in the St. Charles formation at the base of a lithic unit lying between 250 and 273 feet above the last true quartzite of the Worm Creek member, and about 50 feet below the lowest dolomite unit. This 23 foot lithic unit consists of light gray, medium-

grained limestone, limestone coquinas and poorly developed limestone pebble conglomerate, with thick silt partings. The silt weathers tan, pink, maroon and yellow. A few thin silty dolomites may be present in the unit. Robert Bright believes that the material represents the highest occurrence of *Ptychaspis* in the St. Charles formation.

The locality is on the knife ridge north of Mink Creek (due north of Mink Creek Spring) at elevation 7,300 ft., due north of the last 0 on the 6,500 ft. contour, Preston quadrangle, Idaho.

COMPOSITION OF THE FAUNA

The faunule contains fourteen species of trilobites assigned to 10 genera and one subgenus, two species of Gastropoda, a species of articulate brachiopod and several uncommon species of inarticulate brachiopods. With the exception of *Idahoia*, *Pseudagnostus* and *Ptychaspis*, each genus is represented by a single species.

Ptychaspis bullasa, n. sp.
Ptychaspis granulosa (Owen)
Idahoia serapio Walcott
Idahoia wisconsensis (Owen)
Idahoia (*Meeria*) *modesta*, n. sp.
Saratogia fria, n. sp.
Wilbernia pero (Walcott)
Drumaspis walcotti Resser
Minkella americana, n. gen., n. sp.
Bellaspis? oblonga, n. sp.
Taenicephalina globula, n. sp.
Leiostegium? sp. undet.
Pseudagnostus convergens Palmer
Pseudagnostus prolongus (Hall and Whitfield)
Anconochilus idahoensis, n. sp.
Pelagiella sp. undet.
Billingsella cf. *B. plicatella* Walcott
Obolus sp. undet.
cf. *Acrotreta* sp.

Ptychaspis bullasa is overwhelmingly the most common species of the faunule. Forty cranidia, ranging in size from 0.7 mm. to 22 mm. in length, 20 free cheeks and 20 pygidia showing a comparable size range, were sorted out to represent the species; but complete or fragmentary *Ptychaspis* cranidia occur on the pieces of nearly all the specimens in the collection. The cranidium of *P. bullasa* is most similar to that of *P. granulosa* (Owen)—the glabella has the same shape and the outer surface is covered with large granules. It differs in the greater convexity of the glabella, and the greater length and lower convexity of the frontal area. The pygidium which has been associated with this cranidium on the basis of abundance is quite unlike that of *P. granulosa*, but similar in shape of axis and upturned marginal border, to the pygidium associated with *P. tuberosa* Kurtz.

Ptychaspis granulosa (Owen) has been identified from twenty-eight cranidia and eighteen pygidia. The cranidia of the two species can be distinguished consistently only on the essentially vertical position of the frontal area in *P. granulosa*. The lower convexity (sunken position) of the glabella between the fixed cheeks, a supposed specific characteristic of *P. granulosa*, is highly variable and appears to grade imperceptibly into the higher position of *P. bullasa* and *P. striata*. The pygidium of *P. granulosa* is quite distinctive and the well preserved Idaho specimens show that it also had a surface ornamentation of imbricating ridges. Apparently in *Ptychaspis* coarse granules occurred primarily on the cranidium and inner half of the free cheeks, whereas the outer part of the fixed cheeks, and the thorax and pygidium were ornamented by the ridge pattern.

The largest number of genera belong to the Idahoiidae. Although this family is adequately represented in all the cratonic faunas of the *Ptychaspis-Prosaukia* faunizone, its members become especially conspicuous in the faunas in the northern portion of the Cordilleran region of the United States; so much so that one or more *Idahoia* zones may be recognized locally. *I. serapio* is represented by 15 cranidia, showing a size range of holaspid specimens, but very few free cheeks or pygidia. The type material of the species came from Malad, Idaho, and the species has only been reported from Idaho and Montana. *I. wisconsensis* is represented by 20 cranidia, a few free cheeks and pygidia. The cranidia are all small holaspids, none of them over 7 mm. in length. The two species are readily distinguished by the differing ratio of the width (sag) of the preglabellar field/anterior border. No tendency toward intergradation with respect to this feature has been observed. *I. serapio* now appears as a strictly northern Cordilleran species, while *I. wisconsensis* had a much wider geographic distribution. The size limitation on the speci-

mens of *I. wisconsensis* indicates better, probably longer, sorting of this material and suggests that the two species belonged to different ecologic biotas.

A third species represented by 15 cranidia (showing a size range up to 13 mm.), several free cheeks and four pygidia is referred to *Idahoia* (*Meeria*) *modesta*, n. sp. This species and an additional undescribed species from Texas now give a more adequate generic concept of *Meeria*, first described from a high *Conaspis* zone faunule in Oklahoma. The three species show that *Meeria* is very similar to *Idahoia* in the morphology of the exoskeleton yet differs consistently from *Idahoia* (s.s.) in a few minor features. None of these features in itself is of more than specific value, but the combination of them produces a form which cannot readily be placed in *Idahoia* (s.s.). The recognition of *Meeria* as a subgenus of *Idahoia* rather than an independent genus is chosen as best expressing the relationship of the two forms. The present known stratigraphic range of *Meeria* from the top of the *Conaspis* zone to near the top of the *Ptychaspis* subzone substantiates the somewhat less specialized appearance of the exoskeleton, and suggests this form as the ancestral type of *Idahoia*. This clarification of the relationship of *Meeria* removes it from the Parabolinoididae where it was placed by Lochman (1956).

A new species of *Saratogia* is recognized. Since 1935 *Saratogia* has been known primarily by the genotype, *S. calcifera* from the Hoyt limestone of New York. A few fragments have been assigned to *Saratogia* in the central Appalachian region by B. F. Howell but they are too poor for study. The recognition of the Idaho species and several undescribed species from Montana and Texas apparently extends the range from the *Saukia* faunizone down at least to the middle of the *Ptychaspis-Prosaukia* faunizone, and provides a more clear-cut concept of the genus. *Saratogia* is unquestionably close to *Idahoia*—the cephala of the two genera differ in only a few minor details, but the pygidium associated with *S. calcifera* is quite different from the *Idahoia* type. The present known range of *Saratogia* suggests that this genus developed directly from one of the *Idahoia* species in which the anterior facial sutures run nearly straight forward from the palpebral lobe to produce the distinctive narrow (tr) frontal area.

Wilbernia is represented in the faunule by cranidia referred to the genotype species, *W. pero* (Walcott). The number of specimens is small, but shows a wide size range, and the surface preservation of the material is excellent. *W. pero* is a distinctive species with a wide geographic range, from Texas to Minnesota in the central United States, and now in the northern Cordilleran region as well.

The Elviniidae are represented by a single species of *Drumaspis*. The relatively small number of specimens and the poor preservation of the larger specimens is atypical of *Drumaspis* occurrences in the Cordilleran region. Resser's (1942) original description of the genus is the only published material on *Drumaspis*. Resser recognized cranidia of a large number of species distributed from Montana to Idaho and in Oklahoma and Texas, but no pygidia were described. *Drumaspis* is moderately abundant in Resser's material with respect to numbers of individuals, but probably not more than six or seven valid species are present. *D. walcotti* Resser was first described from near Malad, Idaho. *Drumaspis idahoensis* Resser from the same locality, *D. briscoensis* from Alberta, and *D. nitida* from Oklahoma are considered synonyms of *D. walcotti*. The structure of the exoskeleton of this species suggests that it is a median type not far removed from the ancestral form. *Drumaspis* is commonly associated with faunules of the *Ptychaspis* subzone, but it is not known how high the genus may range in the *Prosaukia* subzone.

A new genus *Minkella* is described. It is placed in the Dokimocephalidae, a family previously limited in the shallow shelf assemblages to the *Elvinia* faunizone. *Minkella* is represented by two suites of very similar appearing cranidia which differ only in two minor details. The larger suite of cranidia, showing a good range in size, have a short occipital spine, and a somewhat more convex glabella with deeper glabellar furrows. A smaller suite of cranidia, showing a comparable size range, lack an occipital spine and have a less convex glabella with shallower glabellar furrows. This is the third instance known to the senior author of the

occurrence in Upper Cambrian trilobite populations of cranidia which are essentially similar, differing only in the presence or absence of an occipital spine and a slight change in glabellar convexity, and the associated free cheeks and pygidia are indistinguishable one from the other. Previously these forms were described as different species (Lochman and Duncan, 1944), although Lochman suggested that they might well represent the two sexes of one species. The repeated observation of this phenomenon, and the fact that this collection is a single faunule rarely having more than one species to a genus has convinced the authors that these two suites of specimens should be described as the male and female forms of a single species. Since the determination of the sexes must be based solely on features of the dorsal exoskeleton, the authors have utilized certain characteristics observable in the carapace of the most primitive living Merostomata as the guiding principle. In *Limulus* the sex organs are located in the cephalothorax, and the female is the larger, more robust individual with a broader and somewhat higher cephalothorax. The female is also a slow moving individual. In the *Minkella* specimens the suite of cranidia with the more convex glabella is designated the female form. This form also has an occipital spine. The cephalic spines in trilobites appear to be primitive structures which frequently occur in the meraspid. Their retention in the holaspid may be purely fortuitous, or may give the form some survival advantage. The curved occipital spine might have some protective value to the slow moving female; but in the male mobility is more important, the spine would certainly not be needed and might be a hindrance. As the specimens occur in a coquina it is difficult to draw an accurate conclusion concerning the significance of the relative abundance of the two types. The suites are represented by individuals of comparable size range, so that there is no obvious size sorting. However, we cannot conclude that in this trilobite population the females normally considerably outnumbered the males—even though this is a common situation in many modern Arthropod groups. The observed condition could just as well be interpreted as a seasonal or temporary segregation of the sexes.

The presence of a second species of *Taenicephalina* in this faunule adds another element of similarity to the *Hungaia magnifica* fauna of Quebec. From the latter assemblage there have also been described species belonging to the Dokimocephalidae and other families presumed to be characteristic of the *Elvinia* faunizone. *Taenicephalina* was previously known only by the genotype *T. lechevalieri* (Rasetti, 1945). The cranidia of *T. globula*, n. sp. is very similar to that of the type species, differing only in several small details, and a single small pygidium has been tentatively associated with these cranidia.

Two other species, each represented by a single cranidium, have been described and figured for reference. A single small, 2.5 mm. well-preserved cranidium is named *Bellaspis? oblonga*, n. sp. It most closely resembles *Bellaspis billingsi* Rasetti, genotype and only positively identified species of this genus, from the *Hungaia magnifica* fauna of Quebec. The cranidia of the two species differ in only one feature—in *B. billingsi* the glabella is broad-conical since the dorsal furrows converge slightly anteriorly and the corners and front of the glabella are rounded, whereas in *B? oblonga* the glabella is subquadrate since the dorsal furrows are nearly parallel and the front is straight. Much more material is needed to determine the significant generic characters of *Bellaspis*.

A second fragmentary cranidium has been tentatively referred to *Leiostegium*, a genus characteristic of and previously recorded only from the basal Ordovician. All the observable features of this crandium are the same as those of *Leiostegium*, but more complete cranidia could reveal important distinctions. The present observed resemblances suggest that this earlier species may be an ancestral form.

The Agnostida are represented by two species of the characteristic Franconian genus, *Pseudagnostus*. The larger number of cranidia and pygidia are identified as *P. prolongus* (Hall and Whitfield), a species recorded from the lower part of unit 1 of the Pogonip limestone in the Eureka district, Nevada (Palmer, 1955). Both exterior surfaces and limestone molds are present in the

Idaho material. The species is distinguished by the extreme shallowness (essentially obsolescence) of the dorsal, axial and preglabellar median furrows on cephalon and pygidium exteriors. The limestone molds of the Idaho material show, often in the most minute detail, the features of the ventral (inner) surface of the dorsal exoskeleton. The pattern of muscle scars on cephalon and pygidium (pl. 1, figs. 10–14, text figure 1) is similar to that shown by Palmer for *P. convergens*, but there are several differences. In all the cephala the base of the axial node lies at the exact center of the glabella. On the largest cephalon the anterior muscle scars appear elongate-oval in shape and lie in a diagonal position, while the median arcuate scars show up as actually double with a narrow raised area between the scar depressions. In addition, several of the best preserved limestone molds of cephala and pygidia show a radiating pattern of coarse punctae crossing the cheeks and the pleural regions. The pattern across the cheeks has exactly the same position and arrangement as that of the caecal venations crossing the preglabellar field and free cheeks in regular trilobites. It is reasonable to assume that it represents the trace of an homologous structure.

A second species, identified as *P. convergens* Palmer, is represented by a smaller number of cephala and pygidia. The cephala show on the exterior the more distinct dorsal and preglabellar median furrows mentioned by Palmer as diagnostic of the species. Several interiors show some of the muscle scars and a faint suggestion of the pitting.

In addition to the trilobites there are specimens of a small planospirally coiled gastropod, identified as *Anconochilus idahoensis*, n. sp., a few valves of the articulate brachiopod, *Billingsella* cf. *B. plicatella* Walcott, one valve referred to *Acrotreta*, several small inarticulate valves referred to *Obolus*, and a broken shell of *Pelagiella*. Etching the material with acetic acid produced a residue of 1) trilobite fragments of *Ptychaspis*, *Idahoia* and *Pseudagnostus*, 2) a great abundance of small steinkerns of both *Pelagiella* and *Anconochilus*, 3) some calcareous sponge spicules, 4) stem, plate and brachiole fragments of a cystoid, 5) steinkerns of *Hyolithes*, and 6) a few broken valves of *Billingsella* and *Obolus*.

ECOLOGY OF THE FAUNA

The lithology of the fossil horizon is a poorly developed limestone pebble conglomerate in which the matrix forms 85–90 per cent of the bed. The few small ($\frac{1}{2}$ to $\frac{3}{4}$ inch) dark gray, fine-grained, subangular to subrounded pebbles lie in a matrix composed of trilobite fragments, medium-grained, light gray crystalline limestone and rounded glauconite grains. The very random orientation of the fossils and the occurrence of fossils of all sizes and shapes indicates that the coquina debris was not well sorted before final deposition. The etched residues contain secondary chert of sand grain size and smaller, as well as the fossil debris and glauconite. Little clastic material could be identified and it is silt size and smaller. Land currents were not directly reaching this sea bottom, and such sorting as did occur must have been effected by oscillation waves or slow bottom currents. The faunule must be composed of benthonic species living in the immediate area mingled with nektonic and planktonic species which were over the bottom at the time of their death. R. Bright reports that this material is unusual in the prominence of *Ptychaspis* specimens; and that in most of the fossil coquinas from the St. Charles formation *Idahoia* and/or *Drumaspis* are the conspicuous elements.

The species of this material may be classified in five groups with respect to the original habitat. The species in the first group are believed to represent the benthonic in situ assemblage. *Ptychaspis bullasa* is very common in number of specimens, is represented by a wide size range of both cranidia and pygidia. The species is regarded as the dominant benthonic species inhabiting the area of deposition. *Minkella americana*, although not as abundant, also shows many characteristics of the remains of an indigenous population. The large numbers of *Anconochilus idahoensis* suggest a local population, but the adult size of the species is not known, so that these specimens may represent a sorted assemblage of the smaller individuals.

The second group is composed of benthonic species which are believed to have formed populations on the bottom areas adjoining the site of deposition—*Saratogia fria, Ptychaspis granulosa, Wilbernia pero, Idahoia serapio* and *Idahoia* (*Meeria*) *modesta.* These species are represented by a moderate number of cranidia which show an appreciable size range, though not as great as in group 1, and a few pygidia in some instances. The disarticulated pieces of the exoskeleton have been moved, but the movement was not enough to effect a good size sorting. *Taenicephalina globula* also shows the characteristics of this group, but the limited knowledge of the normal adult size of the genus prevents a definite classification.

A third group is composed of those presumed benthonic trilobite species of which the specimens show the strongest evidence of sorting, *Idahoia wisconsensis, Drumaspis walcotti* and possibly also *Taenicephalina globula.* Only cranidia and pygidia of small size are present, indicating that these specimens have been carried by currents well away from the indigenous bottom sites of the species. The pieces of the larger cranidia of *Drumaspis* which are present have been reduced by fragmentation to a size comparable to that of the small complete cranidia. A mechanical size sorting phenomenon is involved here and not a preference segregation of adolescent individuals with respect to habitat.

The elements of these three groups may be regarded as the normal benthonic populations occupying slightly different sea floor habitats within an areal expanse of 10 to 20 miles radius of the site of deposition of the coquina. At present the nature of the specific habitat niches occupied by the normal benthonic trilobites of these assemblages is not known, but the great abundance and wide distribution of several species of *Idahoia* in the northern Cordilleran region affords an opportunity for study of this problem.

In the fourth group are to be found species which were either relatively rare members of the habitats within this same areal distribution or have been carried a considerable distance from their insitu habitat. All of the brachiopod specimens as well as the few cystoid fragments and calcareous sponge spicules belong to the latter category. All represent sessile benthos living normally on a shallow firm sea bottom. The absence in the etched residues of clastic material above the clay size indicates that this coquina was deposited a considerable distance from any shore region which was furnishing sand for a firm sea floor. The two trilobite species represented by a single cranidium each, *Bellaspis? oblonga* and *Leiostegium?* sp. undet., may have been extremely rare members of nearby trilobite populations or strays from a different environment. The genera to which they have been assigned have never before been recorded from this province.

In group 5 are placed those species which are believed to have been normal members of the pelagic planktonic assemblages of this Upper Cambrian sea—*Pseudagnostus, Pelagiella* and *Hyolithes.* The two species of *Pseudagnostus* are represented by the same number of cephala and pygidia per species, with specimens of *P. prolongus* much more common than those of *P. convergens.* The occurrence of identical numbers of cephala and pygidia representing each species of Agnostid is not readily attributable to selective sorting even though these parts of the exoskeleton are similar in size and shape and the range in growth stages is not wide. The steinkerns of *Pelagiella* and *Hyolithes* show a similar limited size range. It is believed that the shells of these forms constitute an insitu thanatocoenose—an assemblage of those planktonic individuals which ordinarily lived as adults in the overlying waters, but upon death sank toward and settled upon the sea bottom where their decaying bodies could be incorporated in any local coquina.

CORRELATION OF THE FAUNULE

The majority of the genera and species of this faunule comprise a shallow shelf—Pacific province—assemblage readily correlated with the *Ptychaspis* subzone of the Franconian stage. The association of *Ptychaspis granulosa,* the related species *Ptychaspis bullasa, Wilbernia pero* and *Idahoia wisconsensis* suggests a position at or near

the top of the *Ptychaspis granulosa* teilzone of the Upper Mississippi Valley section. The high position is favored because of the prominence of *Ptychaspis bullasa*, a form which may well be the direct ancestor of *Pty. tuberosa* Feniak recorded in Wisconsin from the overlying *Pty. striata* teilzone. Grant (1957) has recorded the same position as the teilzone for *Idahoia serapio* in southwestern Montana. *Ptychaspis striata* Whitfield has been recorded from both north central Montana (Lochman, 1950) and south central New Mexico (Kottlowski, et al., 1956) so that the species apparently was distributed throughout the Cordilleran region and could be expected to occur were the faunule as high as the *Pty. striata* teilzone of Wisconsin. *Drumaspis* occurs in Texas and in Montana (Grant, 1957) in the lower two-thirds of the *Ptychaspis* subzone. The stratigraphic range of *Saratogia* and *Idahoia* (*Meeria*) is not known but the ancestral position of *Meeria* on the *Idahoia* line would suggest a range not beyond the lower part of the *Ptychaspis* subzone.

This faunule is distinctive, when compared to the assemblages known from the *Ptychaspis* subzone in Montana and Wyoming, in the presence of several far western and extracratonic elements. This intermingling of species from both provinces suggests that this faunule lies near the outer edge of the shallow shelf environment, or actually at the boundary with the intermediate environment of the miogeosynclinal realm. Species of the planktonic *Pseudag-*

EXPLANATION OF PLATE 57

FIGS. *1–6—Pseudagnostus convergens* Palmer. *1*, exfoliated cephalon showing anterior muscle scars, ×4, U.S.N.M. 137088. *2*, exfoliated cephalon with well-defined furrows, ×4.7, U.S.N.M. 137088a. *3*, small cephalon with outer surface, ×7, U.S.N.M. 137088b. *4,5*, two exfoliated pygidia showing accessory furrows, long axial node and slight constricting of posterolateral margin, ×6, U.S.N.M. 137088c, U.S.N.M. 137088d. *6*, small exfoliated pygidium, ×7, U.S.N.M. 137088e.

7–16—Pseudagnostus prolongus (Hall and Whitfield). *7*, partially exfoliated cephalon, preglabellar median furrow obsolete, ×5, U.S.N.M. 137089h. *8*, exfoliated cephalon with shallow preglabellar furrow and muscle scars, ×6.4, U.S.N.M. 137089k. *9*, cephalon with outer surface, ×10, U.S.N.M. 137089c. *10,15*, exfoliated pygidia, accessory furrows very faint, short axial node, some muscle scars, ×5, ×4.6, U.S.N.M. 137089g, U.S.N.M. 137089e. *11,12*, exfoliated pygidia, shape of axial lobe indicated by muscle scars and radiating pits, ×3, U.S.N.M. 137089d, 137089i. *16*, partially exfoliated pygidium, ×4, U.S.N.M. 137089f. *13,14*, small cephala, ×10, U.S.N.M. 137089a, U.S.N.M. 137089b.

17–20—Billingsella cf. *B. plicatella* Walcott. *17*, adult ventral valve with good ornamentation, ×1.8, U.S.N.M. 137090a. *18*, immature ventral valve, ×3, U.S.N.M. 137090b. *20*, poorly preserved dorsal valve, ×2, U.S.N.M. 137090c. *19*, hinge of ventral valve, ×10, U.S.N.M. 137090d.

21,22—Leiostegium? sp. undet. profile and dorsal views of single fragmentary cranidium, ×4, U.S.N.M. 137095.

23,24—Bellaspis? oblonga, n. sp. holotype, profile and dorsal views of a single well-preserved cranidium, ×5, U.S.N.M. 137096.

25–33—Anconochilus idahoensis, n. sp. *25*, paratype, specimen showing axial ornamentation and selenizone, ×10, U.S.N.M. 137092g. *26,27*, paratypes, side views of two specimens showing symmetrical coiling, ×10, U.S.N.M. 137092f, U.S.N.M. 137092e. *28*, paratype, small specimen with well preserved selenizone, ×9, U.S.N.M. 137092c. *29,30*, holotype, dorsal and side views of large specimen, ×10, U.S.N.M. 137091. *31*, paratype, steinkern showing trace of selenizone, ×10, U.S.N.M. 137092b. *32*, paratype, broken specimen showing inner whorls, ×10, U.S.N.M. 137092a. *33*, paratype, large specimen showing outline of aperture, ×10, U.S.N.M. 137092d.

34–43—Taenicephalina globula, n. sp. *34,37*, paratypes, cranidia with some outer surface, ×6, U.S.N.M. 137094a, 137094b. *35*, paratype, exfoliated cranidium showing trace of coarse granules from outer surface, ×4.3, U.S.N.M. 137094c. *38,42,43*, holotype, front, profile and dorsal views of small, well-preserved cranidium, ×6, U.S.N.M. 137093. *39*, paratype, small associated pygidium, ×7, U.S.N.M. 137094d. *36*, paratype, largest cranidium, ×3.5, U.S.N.M. 137094e. *40*, paratype, broken cranidium with outer surface, ×4, U.S.N.M. 137094f. *41*, paratype, large broken cranidium, glabella appears more broadly conical than on other specimens, ×4, U.S.N.M. 137094g.

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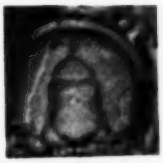
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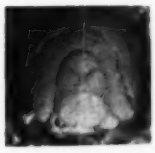
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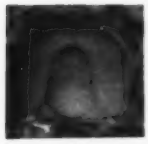
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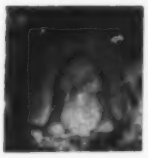
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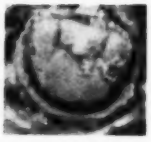
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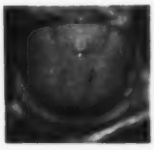
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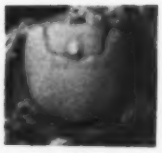
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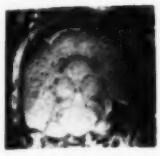
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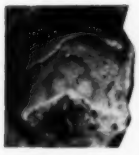
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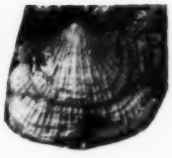
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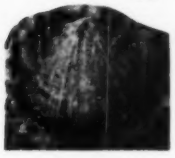
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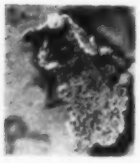
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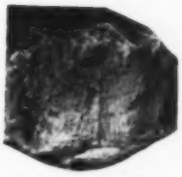
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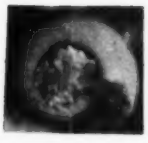
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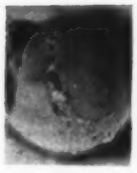
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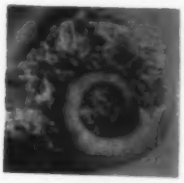
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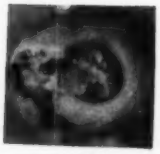
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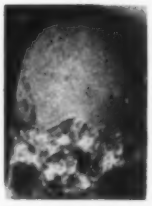
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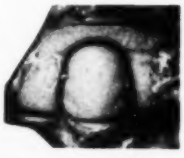
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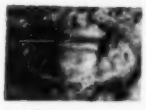
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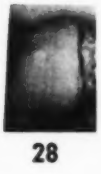
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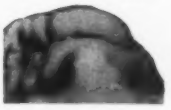
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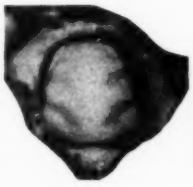
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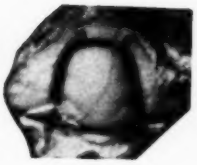
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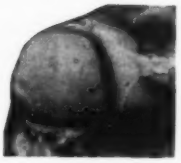
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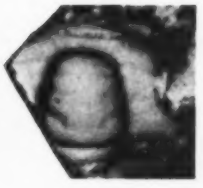
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nostus would be expected to have a wider geographic range than benthonic forms. Both of the species in this faunule occur abundantly in the Eureka district, Nevada. Palmer (1955) reports *P. prolongus* associated with the *Elvinia* faunizone in the lower part of unit 1 of the Pogonip limestone and *P. convergens* with an assemblage comparable to the *Hungaia magnifica* fauna in the upper part of unit 1 of the Pogonip. The association of both species in this faunule suggests that *P. prolongus* had a long stratigraphic range in the Franconian, a characteristic of many extracratonic forms.

Taenicephalina and *Bellaspis* have been previously reported only from the *Hungaia magnifica* fauna of the Lévis boulders of Quebec where they are known only by the genotype species. This fauna now appears to range in the extracratonic environment from the middle Franconian into the lower part of the Trempealeauan (Lochman-Balk and Wilson, 1958). These particular genera have not yet been reported from the Eureka district, but since other elements of the *Hungaia* fauna are present in this region, it is to be expected that these genera entered Idaho from the west. The new genus *Minkella*, as a member of the Dokimocephalidae, is an additional extracratonic element. The Dokimocephalidae appear in and are a conspicuous component of the assemblages of the *Elvinia* faunizone in all three biofacies across North America. They disappear from the shallow shelf and intermediate environments during *Conaspis* zone time; but the family apparently persisted in the extracratonic environment, as members of the family are known from the *Hungaia magnifica* fauna of Quebec.

The specimen named *Leiostegium?* sp. undet. probably represents a fourth extracratonic element in this faunule. It is very similar to *Leiostegium* and is regarded as a possible ancestral form. *Leiostegium* appears in zone D of the Gasconadian and from its faunal associations appears to be an extracratonic migrant into the Colorado and New Mexico sections from which it has been recorded. It has never been reported from Zones A to C either in Utah (Ross, 1951) or eastern Nevada (Hintze, 1952). Conse-

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EXPLANATION OF PLATE 58

FIGS. *1–20*—*Minkella americana*, n. gen., n. sp, *1,5*, paratype, dorsal views of mold of the impression and the replica of small cranidium showing occipital spine, ×2.6, U.S.N.M. 137098e. *2,3*, holotype, dorsal and profile of medium-sized cranidium, ♀ form, ×1.8, U.S.N.M. 137097. *7,8*, paratypes, free cheeks, ×1.8, U.S.N.M. 137098i, U.S.N.M. 137098h. *18*, paratype, meraspid pygidium, ×10, U.S.N.M. 137098k. *20,19*, paratypes, fragmentary holaspid pygidia, ×6, ×2.4, U.S.N.M. 137098j, U.S.N.M. 137098L. *9,10*, paratype, smallest meraspid cranidium, ×11, ×20, U.S.N.M. 137098a. *11*, paratype, a larger meraspid cranidium, ×10, U.S.N.M. 137098b. *13,12*, paratypes, early holaspid cranidia, ×8.5, ×7, U.S.N.M. 137098c, U.S.N.M. 137098d. ♂ form of cranidium, *6,4*, paratype, profile and dorsal views of exfoliated medium-sized cranidium, ×1.5, U.S.N.M. 137098n. *16,17*, paratypes, dorsal views of two more cranidia, ×2.3, ×1.8, U.S.N.M. 137098o, U.S.N.M. 137098m. ♀ form of cranidium, *14*, paratype, small cranidium with finely granular outer surface, ×4, U.S.N.M. 137098g. *15*, paratype, another cranidium, ×5, U.S.N.M. 137098f.

21–42—*Ptychaspis bullasa*, n. sp. *38,39,40*, holotype, front, profile, and dorsal views of medium-sized cranidium, ×2, U.S.N.M. 137099. *42*, paratype, large, partially exfoliated cranidum, ×2, U.S.N.M. 137100n. *41,37*, paratypes, smaller cranidia, ×3, ×2, U.S.N.M. 137100i, U.S.N.M. 137100k. *36*, paratype, free cheek, ×2, U.S.N.M. 137100j. *27,30,34*, paratypes, exfoliated pygidia, ×2, ×2.5, ×3, U.S.N.M. 137100L, U.S.N.M. 137100s, U.S.N.M. 137100h. *33*, paratype, mold of pygidium showing some outer surface, ×2, U.S.N.M. 137100o. *31*, paratype, small holaspid pygidium with unbroken border on right side, ×6, U.S.N.M. 137100p. *21,22*, paratypes, meraspid cranidia, ×10, U.S.N.M. 137100a, U.S.N.M. 137100b. *23,24,26*, paratypes, early holaspid cranidia, ×10, ×6, ×6, U.S.N.M. 137100c, U.S.N.M. 137100d, U.S.N.M. 137100e. *35*, paratype, well-preserved, medium-sized cranidium, ×4, U.S.N.M. 137100r. *25*, paratype, associated hypostome, ×2, U.S.N.M. 137100m *28,29*, paratypes, meraspid pygidia with thoracic segments, ×8, U.S.N.M. 137100f, U.S.N.M. 137100g, on smallest (fig. 29) ends of segments still show as spines along lateral margins, *32*, thoracic pleuron referred to *Ptychaspis*, ×2.5, U.S.N.M. 137100t.

quently the ancestral genus of *Leiostegium* would be expected to be a normal element of the extracratonic environment.

SYSTEMATIC DESCRIPTIONS

Phylum ARTHROPODA
Class TRILOBITOMORPHA
AGNOSTIDA
PSEUDAGNOSTUS CONVERGENS Palmer
Pl. 57, figs. 1–6

Pseudagnostus convergens Palmer, 1955, p. 96, pl. 19, figs. 14,15.

A small number of cephala and pygidia can be distinguished from the much more numerous specimens of *Pseudagnostus prolongus* Palmer in this material by their possession of features which have been mentioned by Palmer as diagnostic of *P. convergens.* In the cephalon the dorsal furrow is distinct and the preglabellar median furrow is rather deep directly in front of the glabella. Most of the cephala show a smooth exterior, but a few showing the interior have the muscle scars partially preserved and a faint suggestion of pitting. The cephala referred to *P. prolongus* show these features more clearly.

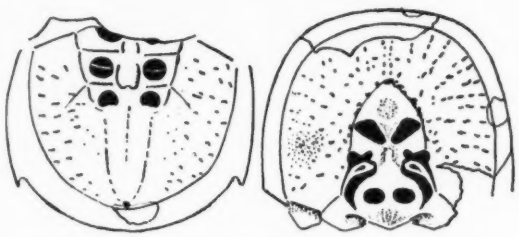
The pygidia show the long prominent axial node, and the rather distinct accessory furrows which diverge at a low angle from the second segment around the pseudolobe. One peeled pygidium shows the true axial lobe with faint muscle scars. However, the posterior margin of most of these pygidia shows the sides much more rounded than in the holotype pygidium, which gives the impression of having the sides slightly crushed together. This is the only observable difference and the authors are loath to describe a new species when all the other features are in such close agreement.

The species is represented by five cephala, ranging from 1.5 to 3.75 mm. in length and five pygidia, ranging from 1.5 to 3 mm.

Figured specimens: cephala, U.S.N.M. 137088, 137088a–b; pygidia, U.S.N.M. 137088c–e.

PSEUDAGNOSTUS PROLONGUS
(Hall and Whitfield)
Pl. 57, figs. 7–16

Agnostus prolongus HALL & WHITFIELD, 1877, p. 230, pl. 1, figs. 30,31.



TEXT-FIG. *1*—Sketch of muscle scar pattern on cephalon and pygidium of *Pseudognostus prolongus* (H. and W.)

Pseudagnostus prolongus (Hall and Whitfield) PALMER, 1955, p. 98, pl. 19, figs. 17,18,22.

Remarks: The more abundant *Pseudagnostus* species has been referred to *P. prolongus* (Hall and Whitfield) because the exterior surface of the cephala and pygidia are similar in all features to the cotypes and plesiotypes figured by Palmer (1955). The furrows of the exoskeleton are very shallow, particularly so on the exterior where they are nearly obsolete. A number of these specimens are exfoliated, and it can be seen that on the interior the entire course of the furrows is discernible, although they are shallow. The small size of the axial nodes on both cephala and pygidia is also a distinctive feature of the species.

Although the specimens are preserved in ordinary dark brown limestone, the limestone molds of the interior have retained, for some unknown reason, often in the most minute detail, the pattern of the muscle scars and a radiating pattern of coarse punctae which are assumed to be the trace of rows of caecal tubes or undulating caecal venations. In the cephalon the radiating pattern extends out from the dorsal furrow across the cheeks to the border furrow, in the same arrangement shown by the caecal venations in regular trilobites. On several pygidia radiating punctae also cross the pleural lobes in the area bounded by the dorsal furrow, the accessory furrows and the border furrows.

The muscle scars are well preserved on both cephala and pygidia (text-fig. 1). The pattern is similar to that illustrated by Palmer (1955, pl. 20, fig. 13) for *P. convergens*, but there are several distinct differences, some of which may be attributed to specific variation, but others to the ex-

cellent preservation in this material. On the largest cephalon, it may be noted that the anterior muscle scars are elongate-oval and lie in a diagonal position, while the median arcuate scars are actually double with a narrow raised area between the scar depressions. The other muscle scars are the same in size and position as shown by Palmer. On all these cephala the base of the axial node lies at the exact center of the glabella, evenly spaced between the inner ends of the anterior and the median scars.

One pygidium with a patch of the outer surface on an anterior pleural lobe shows a few coarse longitudinal ridges as a surface ornamentation. Several exfoliated pygidia show the outline of the axial lobe, which appears to be the same as that figured by Palmer (1955, pl. 20, figs. 11,14) for *P. communis*.

P. prolongus (Hall and Whitfield) is reported by Palmer as characterizing the *Elvinia* zone in the Eureka district, Nevada. However, no significant differences can be detected between the specimens illustrated and described by Palmer and those in this material; it is assumed therefore that the species does have a long range, at least in the central Cordilleran region.

Twenty-one cephala, ranging in size from 1 to 4 mm. in length, and the same number of pygidia, ranging from .75 to 4 mm. in length, have been obtained.

Figured specimens: Cephala, exteriors, 137089a,b,c; Cephala, exfoliated, U.S.N.M. 137089h,k; Pygidia, exteriors, U.S.N.M. 137089f; Pygidia, exfoliated, U.S.N.M. 137089d,e,g,i.

Family MARJUMIIDAE
BELLASPIS? OBLONGA, n. sp.
Pl. 57, figs. 23,24

Cranidium quadrate in outline; glabella subquadrate, anterior corners rounded, front straight, moderately convex (flat across center and downsloping anteriorly), two pairs of distinct glabellar furrows, dorsal furrow narrow, shallow, occipital furrow distinct, occipital ring convex, preglabellar field narrow, anterior border furrow distinct with prominent median inbend, anterior border convex, wider at center; fixed cheek—anterior area narrow, downsloping, eye ridge obsolete, anterior facial suture diverging, palpebral area slightly convex, horizontal, about 1/3 glabellar width, palpebral lobe medium size, anterior to center of glabella, posterior area narrow (ex sag), 2/3rds length (tr) of occipital ring.

Outer surface may be finely granular.

Free cheek and pygidium not known.

Remarks: The single small, well-preserved cranidium representing this species cannot be accurately placed as to genus; but it is recognized as a distinct species since it can be shown that it is not a small specimen of one of the other species in this faunule. The cranidium resembles most nearly in general appearance *Bellaspis billingsi* Rasetti described (1945) from the *Hungaia magnifica* fauna in boulders in the Lévis conglomerate. It differs from that species (the genotype and only positively identified species of *Bellaspis*) in the nearly parallel-sided glabella. It may well be that when this genus is better understood, there may be found to be a gradational series from parallel-sided to broadly conical glabella within the generic group, such as is known to occur in the *Leiostegium-Lloydia* suite of species. At present, however, the generic assignment must be questioned.

Type: holotype, cranidium—U.S.N.M. 137096.

Family LEIOSTEGIIDAE
LEIOSTEGIUM? sp. undet.
Pl. 57, figs. 21,22

Cranidium quadrate in outline; glabella rectangular, sides tapered only slightly to broadly rounded front, moderately convex, no glabellar furrows, dorsal furrow narrow but deep along sides, narrow and shallower across front, two pits at anterior end of furrow—deepest pit at antero-lateral corners of glabella, a second pit a short distance back—occipital furrow deep, occipital ring broad, convex, no preglabellar field, narrow, convex border, anterior border furrow at sides only, running into preglabellar furrow; fixed cheek—anterior area convex, downsloping, crossed by a low, curved ridge extending from raised area between the two anterior pits, palpebral area flat, upsloping, between 1/3 and 1/4 glabellar width, palpebral lobe broken, but located posterior to center of glabella, posterior area broken, apparently narrow (ex sag).

Outer surface of glabella and fixed cheeks covered with coarse granules, anterior border with a few narrow, transverse ridges; inner surface apparently smooth.

Remarks: Only a single fragmentary cranidium, 4.75 mm. in length, was found. It checks closely in all observable features with *Leiostegium*, including the paired anterior pits which seem to be a unique feature to *Leiostegium*. But the generic assignment is questioned because better material is needed and *Leiostegium* has never been recorded below the basal Ordovician. It is possible that this fragment may represent an ancestral genus of *Leiostegium* since this is a probable horizon at which such a form could appear. Should more complete material indicate that the genus was *Leiostegium* it would greatly extend the range of the genus.

Figured specimen: cranidium, U.S.N.M. 137095.

Family Dokimocephalidae
Minkella, new genus

Cephalon ovate; glabella broad-conical with straight front, three pairs of curved glabellar furrows, all furrows broad, distinct, preglabellar field and anterior border separated by distinct anterior border furrow, eye ridge weak, occipital spine may be present; fixed cheek horizontal to upsloping —palpebral area about one-fourth glabellar width, eye medium size, opposite center of glabella, posterior area narrow (ex sag), about 2/3rds length (tr) of occipital ring. Free cheek elongate with medium-length genal spine.

Pygidium narrow-transverse, convex, axis strongly convex with short post-axial ridge; 3 axial rings and terminal portion with median depression, pleural regions convex, 3 pleurae with distinct interpleural grooves and pleural furrows, very weak border furrow, narrow border.

Outer surface finely granular with narrow, parallel ridges on anterior and lateral borders of cephalon; inner surface smooth with caecal venations on ocular platform and preglabellar field.

Genotype: Minkella americana, n. sp.

Remarks: Minkella appears to be a member of the Dokimocephalidae and is so similar to *Kindbladia* in the structure of the cephalon, that it seems quite possible that it may be a direct lineal descendant of that genus. The shape and convexity of the glabella is identical to that of *Kindbladia* except that there appears to be a stronger tendency in the *Minkella* individuals for the front of the glabella to flatten, a feature which is present, but not common, in *Kindbladia*. The palpebral lobes are the same size and in the same position in both genera, and the structure of the frontal area is similar, but the anterior margin is rounded in *Minkella* instead of bluntly pointed. The major distinction between the two genera lies in the position of the facial suture. In *Minkella*, although the facial sutures have the same course, they lie nearer the center of the cranidium so that the fixed cheek is narrower and the suture cuts quite close to the dorsal furrow at the position of the eye ridges. The palpebral area is one-fourth or less the glabellar width in *Minkella*, rather than one-third as in *Kindbladia*. A minor but interesting distinction is the presence in *Minkella* of only two bilaterally symmetrical pits in the anterior border furrow, as compared to the three pits in *Kindbladia*. It is believed that the bilaterally symmetrical pair on a line with the dorsal furrows in *Kindbladia* are homologous to the pair in *Minkella*.

Only a few fragmentary pygidia can be associated with these cranidia. They show the structure characteristic of the Dokimocephalidae—a narrow, transverse shape with strongly convex axis and post-axial ridge, 3 axial rings and pleurae, narrow border and faint border furrow. In the smaller pygidia the course of the pleural furrows and interpleural grooves is strikingly similar to that of the *Burnetiella* pygidia, but the larger *Minkella* pygidia show a better defined border. The ornamentation of the outer surface is the same fine granules, closely spaced, as occurs on the Dokimocephalidae.

The single, well represented species, *M. americana*, n. sp. is described from this faunule.

Minkella americana, n. sp. ♀
Pl. 58, figs. 1–3,5,7–15,18–20

Cranidium elongate rectangular; glabella conical, strongly convex with rounded an-

terior corners and nearly straight front, three pairs of distinct, arcuate glabellar furrows, anterior pair short, shallow, posterior pairs longer, deeper, S1 almost complete; largest cranidia with low median keel on interior; dorsal and occipital furrows broad, deep on interior, shallow on exterior, occipital ring convex with short occipital spine; preglabellar field convex, downsloping, anterior border furrow broad with an oval pit containing 3–4 granules on each side of midlength on interior, on exterior furrow may show slight median inbend only; anterior border convex, subtriangular; fixed cheek—palpebral area horizontal to slightly upsloping, one-fourth glabellar width, palpebral lobe flat, crescentic, opposite center of glabella, posterior area narrow (ex sag), 2/3rds length (tr) of occipital ring; posterior facial suture runs for short distance straight posteriorly before curving outward and back to cut posterior margin.

Free cheek elongate with medium length genal spine, lateral border convex, lateral furrow broad, shallow; ocular platform convex, slightly downsloping, lateral and posterior furrows not meeting at genal angle.

Pygidium narrow-transverse, moderately convex; axis strongly convex, nearly parallel-sided, 3/4ths length with broad post-axial ridge, 3 axial rings and terminal portion, pleural regions same width as axis anteriorly, downsloping, 3 pleurae, pleural furrows and interpleural grooves distinct, posteriorly curved at ends, faint border furrow not crossing post-axial ridge, border narrow, flat, slightly downsloping.

Inner surface smooth, with 3–4 granules in each oval pit on anterior border furrow, and caecal venations on preglabellar field; outer surface covered with fine granules arranged in a radiating pattern across the preglabellar field, granules merging into several low ridges parallel the margin on the borders of the cephalon.

Remarks: The species is recognized in the material by approximately 35 cranidia which are identical in every specific feature except that the more numerous forms possess a short occipital spine and a somewhat more convex glabella with more distinct glabellar furrows. A suite of five cranidia cover a comparable growth range, but have a less convex glabella and lack an occipital spine. This is the third instance in Upper Cambrian trilobite assemblages known to the senior author of the occurrence within the same population of forms in which the exoskeletons are essentially identical except for a slight difference in glabellar convexity and the presence or absence of an occipital spine. In the other instances—*Arapahoia aspinosa* vs. *A. neihartensis*, and *Cedarina prima* vs. *C. cordillerae* (Lochman and Duncan, 1944) the several forms were described as different species although Lochman suggested that they might represent different sexes of the same species. The continued occurrence of this situation has convinced the senior author that sexual differentiation is the correct explanation for the two forms and that they should be recognized and described as such.

The kind and the very slight degree of differentiation observed in the exoskeleton is consistent with our knowledge of the modern Arthropoda most closely related to the Trilobita—the primitive Merostomata. In *Limulus* the female is the more robust individual with a larger, more convex cephalothorax since the ovaries as well as the other vital organs are located in this part of the body. The known morphology of the Trilobita indicates that the vital organs were also concentrated in the cephalon. The retention of a spine on the cephalon for protection of this part of the body would be more significant in the female than in the males in which a more progressive body structure affording the greatest possible mobility was more important. As the material occurs in a coquina no conclusions can be drawn concerning the relative abundance of the forms.

The form here described, with the occipital spine, is regarded as the female. About 27 cranidia show the distinguishing features and 2 free cheeks and 3 pygidia have been included in this suite. The cranidia range in size from .75 mm. in length (sag) to 15 mm. and the pygidia from 2 mm. to 9 mm. The smaller meraspid individuals and the small holaspids very probably were not mature sexually, but all seem to possess the more primitive occipital spine as would be expected. In the meraspid cranidia under 1 mm. in length the glabella is long, the palpebral area 2/3rds the width of glabella

and slightly downsloping, the preglabellar field very narrow and all the furrows well-defined. The eye ridge is strong and the palpebral lobe proportionately larger than in adult holaspid. Through the early holaspid stages (1 mm. to 3 mm.) a gradual broadening of the glabella to the typical conical shape, and a decrease in width and flattening of the palpebral areas, and an increase in width of the preglabellar field can be traced until the diagnostic specific features of the adult holaspid cranidium have been obtained. The fine granules can be observed on the smallest known specimens.

This genus may be rather widespread in the late Franconian faunas of the Cordilleran region. The figures of the poorly preserved cranidia which have been assigned to "*Taenicephalus*" *megalops* Kobayashi by Kobayashi (1938) and Wilson (1954, 1956) suggest that some of these specimens may be found to belong to *Minkella* when adequately preserved material has been obtained.

Types: holotype—cranidium, U.S.N.M. 137097; paratypes—cranidia, U.S.N.M. 137098a–g; free cheeks, U.S.N.M. 137098h,i; pygidia, U.S.N.M. 137098j,k,l.

MINKELLA AMERICANA, n. sp. ♂
Pl. 58, figs. 4,6,16,17

The cranidium of this form is identical in all specific features to that of the female form except that the glabella is less convex, the glabellar furrows are shallower, and there is no occipital spine but only a small median node on the occipital ring.

Remarks: A suite of five cranidia ranging in size from 2 mm. to 15 mm. in length (sag) show these characteristics.

Types: paratypes—cranidia, U.S.N.M. 137098m–o.

Family ELVINIIDAE
DRUMASPIS WALCOTTI Resser
Pl. 60, figs. 1–14

Drumaspis walcotti RESSER, 1942, p. 28, pl. 4, figs. 37–41.
Drumaspis idahoensis RESSER, 1942, p. 29, pl. 4, figs. 32–36.
Drumaspis briscoensis RESSER, 1942, p. 30, pl. 5, figs. 6–8.
Drumaspis nitida RESSER, 1942, p. 34, pl. 5, figs. 34–35.

Supplementary description: Cranidium with glabella almost quadrangular, tapered very slightly to rounded anterior corners, three pairs of glabellar furrows, anterior pair short, shallow, posterior pairs deep, curved, usually complete, occipital furrow distinct, occipital ring convex with small median node, preglabellar field very narrow, flat, slightly downsloping, anterior furrow narrow, very shallow, anterior border narrow, subtriangular, curving up, then over and down to rounded anterior margin; fixed cheek—anterior area very narrow, palpebral area one-third glabellar width, convex, downsloping, palpebral lobe over medium size, opposite center of glabella, palpebral furrow distinct, posterior area triangular, 2/3rds length (tr) of occipital ring; anterior facial suture a smooth curve along sides of frontal area.

Free cheek with short genal spine, ocular platform convex, narrow anteriorly, increasing in width posteriorly, lateral furrow broad and shallow posteriorly, deepening anteriorly, lateral border of medium width.

Pygidium semicircular, axis very convex, 2/3rds length of pygidium with post-axial ridge continuing to margin, 3 axial rings and terminal portion with distinct median depression, dorsal furrow shallow; pleural platform nearly horizontal, 2 or 3 pleural furrows and interpleural grooves which curve across the faint border furrow onto the flat, medium-width border, posterior margin with slight median inbend.

Inner surface smooth; outer surface of cephalon with fine granules on glabella and fixed cheeks, granules merge with low irregular ridges over ocular platform and occipital ring, and pass into more distinct ridges paralleling the margins on the anterior and lateral borders and the genal spine; outer surface of pygidium with fine granules on axis and pleural platforms, border with ridges paralleling margin.

Remarks: Nineteen cranidia, several free cheeks and nine pygidia have been referred to this species. The cranidia range in size from 1.5 to 8 mm. in length (sag), and in the smaller holaspids the glabella appears longer and narrower because of the lesser convexity of the anterior portion while in the larger cranidia the increased convexity of the anterior lobe gives the glabella a nearly quadrangular shape. The amount of expansion of

the anterior lobe is suspected of being variable in the normal population as several broken cranidia suggest a slightly more tapered anterior course of the dorsal furrow, but show the same structure of the preglabellar field and border.

The pygidia range in length (sag) from 1 mm. to 3 mm. This is the first time that a pygidium has been associated with the genus. This pygidium is quite different from the other types, such as *Ptychaspis* and *Idahoia*, which are well known and common in the assemblages. It also shows a very similar surface ornamentation to that of the cranidium of *Drumaspis*.

Drumaspis walcotti is the genotype of *Drumaspis* and was first described from Two Mile Canyon, Wasatch Mountains, Idaho about 20 miles west of the Mink Creek locality. Examination of the various species described by Resser in 1942 revealed that the holotype cranidia of several other species were conspecific with the cranidia of *D. walcotti*. These species have been indicated in the synonymy. *D. walcotti* would appear to have been well chosen as a genotype. It is quite abundant in the general type area and would appear to have been widespread throughout the Cordilleran region and extended southward into the Oklahoma region.

Figured specimens: cranidia, U.S.N.M. 137106a-d,g,h,k,l,m; free cheeks, U.S.N.M. 137106i,j; pygidia, U.S.N.M. 137106n,o.

Family IDAHOIIDAE
IDAHOIA SERAPIO Walcott
Pl 60, figs. 28–36

Idahoia serapio WALCOTT, 1925, p. 96, pl. 19, figs. 1–12.

Supplementary description: Cranidium rectangular; glabella low, truncato-conical, width (tr) at base equals length, three pairs of faint short glabellar furrows, occipital furrow broad, shallow sinuous, occipital ring with broad based, upcurved occipital spine and distinct median node, dorsal furrow narrow, distinct; preglabellar field moderately downsloping, same width (sag) as anterior border, anterior border furrow broad with a row of granules along posterior edge and making an obtuse angle at the midlength, anterior border flat, downsloping, with slight anterior upcurve, anterior margin tending to be bluntly pointed; fixed cheek—palpebral area one-third glabellar width, flat, slightly upsloping, palpebral lobes medium size, nearly opposite center of glabella, palpebral furrow broad, shallow, broad faint eye ridge, posterior area narrow (ex sag), about ⅔ length (tr) of occipital ring; anterior facial suture diverging at a 40° angle, crossing anterior furrow as a broad, smooth curve, cutting anterior margin near midlength.

Outer surface of free cheek and cranidium marked by "bertillon" wrinkles on glabella, fixed cheeks and ocular platform, changing to ridges paralleling the margin on the borders; the row of granules on the anterior furrow is on the inner surface, and is subdued and indistinct on the outer surface; inner surface punctate with caecal venations on preglabellar field and ocular platform.

Remarks: Twenty-one cranidia, ranging in size from 2.5 mm. to 20 mm., and one free cheek represent this species. Both cranidia and free cheek agree in structure with those of the type lot from Malad, Idaho. One cranidium appears to have a slightly narrower (sag) anterior border and may indicate some intraspecific variation. Although several free cheeks were obtained, no pygidia could be associated with these cranidia.

A supplementary description of the cranidium is given which brings out the particular features which are now known to be diagnostic of this species as distinct from other species of *Idahoia*. At the time Walcott described the species, the generic description was allowed to stand for this species also.

Figured specimens: cranidia, U.S.N.M. 137112a,c–g; free cheek, U.S.N.M. 137112b.

IDAHOIA WISCONSENSIS (Owen)
Pl. 59, figs. 12–32

Crepicephalus? wisconsensis OWEN, 1852, Tab. 1, fig. 13, named and figured.
Idahoia wisconsensis (Owen) LOCHMAN, 1950, p. 329, pl. 46, figs. 11–13; BELL, FENIAK & KURZ, 1952, p. 189, pl. 37, figs. 3a–f (for synonymy to date). BERG, 1953, p. 566, pl. 61, fig. 11.

Supplementary description: Pygidium transverse, axis convex, tapered about 2/3rds length to a narrowed end continuing

onto the border in a post-axial ridge, 3 axial rings and terminal portion, pleural platform nearly flat, same width as axis, 3 pleurae, distinct interpleural grooves which may continue on to border, shallower pleural furrows stopping at the narrow shallow marginal furrow, border wide, flat posteriorly, slightly concave laterally.

Outer surface of exoskeleton with narrow imbricating ridges in "bertillon" pattern; ridges becoming alined to the lateral margins on the anterior border, the borders of the free cheeks and the border of the pygidium.

Remarks: The species is represented by 25 cranidia, all of them small holaspids, ten free cheeks and two pygidia. It is surprising that most of the cranidia are small size, since the other species of *Idahoia* are represented by larger cranidia as well as small ones. The suites of cranidia representing this species and *I. serapio* in this material show that they are two quite distinct species which may occur together in the same locality and in no way are geographic variants as suggested by Bell, Feniak and Kurz (1952).

The cranidia range in size from 0.875 mm. to 8 mm. in length (sag), excluding the occipital spine, which appears to have been rather low and short in length. On one of the smaller cranidia (1.25 mm.) the three pairs of short glabellar furrows and the eye ridges are quite distinct. It would appear from these small cranidia that all the furrows are more distinct, and the convexity slightly higher in the early holaspids, and that with increase in size, the glabella becomes lower and the furrows much fainter.

A number of small cranidia of the same size are illustrated to show the individual variation which may occur in the species. The front of the glabella may vary from narrow rounded to wider so that some glabellas appear more nearly truncate, and the depth of the axial furrow may be medium to shallow.

Figured specimens: cranidia, U.S.N.M. 137101a-m,o,t; free cheeks, U.S.N.M. 137101n,p; pygidia, U.S.N.M. 137101q,r,s

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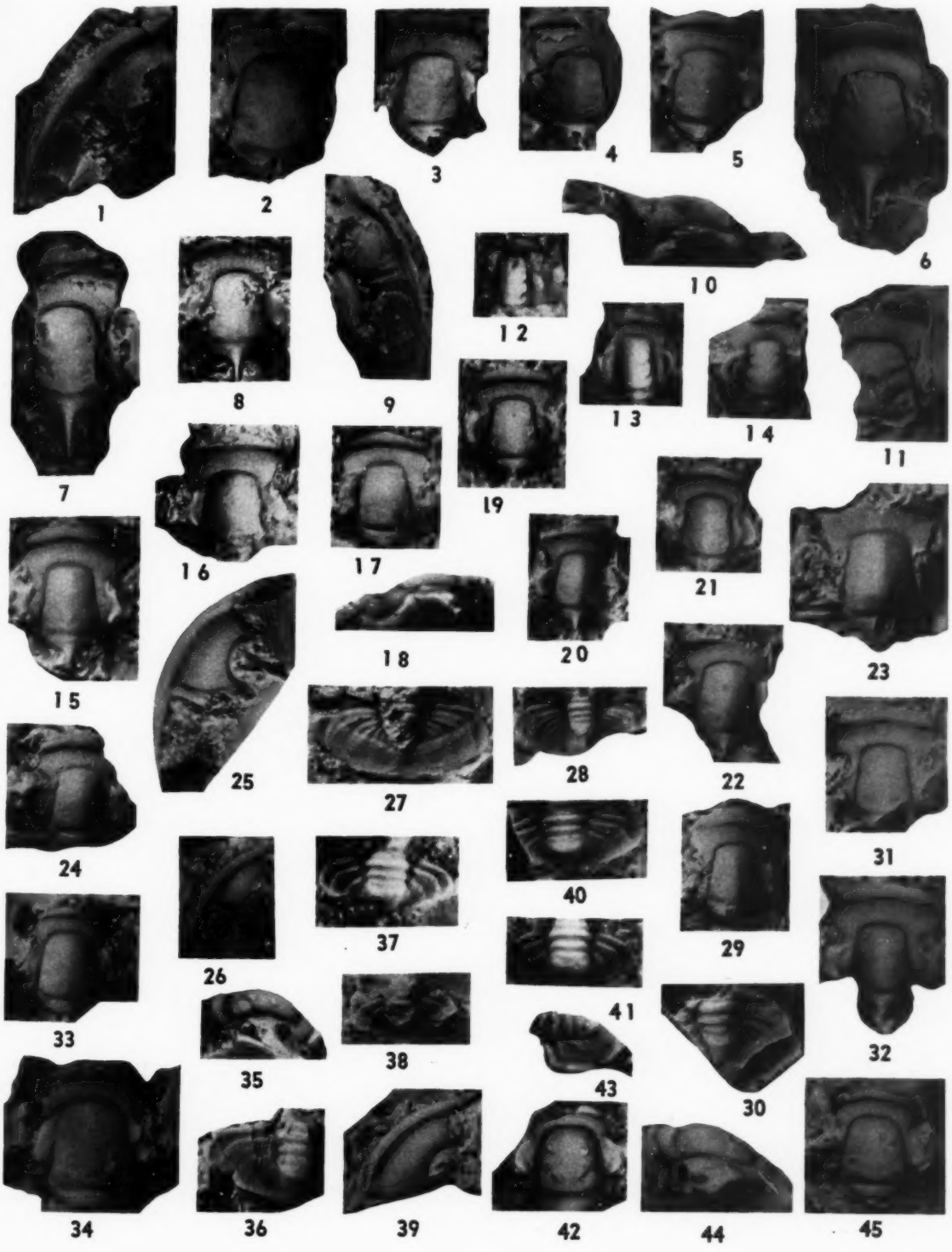
EXPLANATION OF PLATE 59

FIGS. *1–11*—*Saratogia fria*, n. sp. *1*, paratype, large free cheek, ×1.5, U.S.N.M. 137103f. *2,5*, paratypes, dorsal views of two medium-sized cranidia, ×1.5, ×4.4, U.S.N.M. 137103a, U.S.N.M. 137103d. *3*, paratype, dorsal view of smallest cranidium, ×4, U.S.N.M. 137103b. *4,7*, paratypes, dorsal views of two broken cranidia, ×2, ×2.2, U.S.N.M. 137103c, U.S.N.M. 137103e. *10,6*, holotype, profile and dorsal views of best cranidium, ×1.6, U.S.N.M. 137102. *8*, paratype, dorsal view of small cranidium, ×3, U.S.N.M. 137103h. *9*, associated free cheek, ×1.3, U.S.N.M. 137103g. *11*, paratype, medium-sized, crushed cranidium, ×3, U.S.N.M. 137103k.

12–32—*Idahoia wisconsensis* (Owen). *12*, meraspid cranidium, ×11, U.S.N.M. 137101a. *13,14, 17,19,21,23*, progressive growth stages of smallest holaspid cranidia, 1.25 to 3 mm. in length, ×10, ×7, ×10, ×10, ×7, ×8, U.S.N.M. 137101b,c,d,e,f,g. *20,22,32*, small cranidia of same size to show differences caused by individual variation and preservation, ×5, ×5.5, ×5, U.S.N.M. 137101h,i,j. *15,18*, dorsal and profile of small, well-preserved cranidium, ×6, U.S.N.M. 137101o. *16,24,31*, three larger cranidia, ×5, ×4, ×4, U.S.N.M. 137101L, k,m. *29*, largest cranidium found, ×2, U.S.N.M. 137101t. *25,26*, two associated free cheeks, ×4, U.S.N.M. 137101n,p. *27,28,30*, three associated pygidia, medium-sized and small holaspid, and largest fragment, ×4, ×6, ×2, U.S.N.M. 137101r,q,s.

33–45—*Idahoia* (*Meeria*) *modesta*, n. sp. *33*, paratype, dorsal view of cranidium with weathered inner surface, ×5, U.S.N.M. 137105a. *34*, paratype, dorsal view of larger peeled and weathered cranidium, ×3, U.S.N.M. 137105c. *44,45*, paratype, profile and dorsal views of well-preserved, peeled cranidium, ×5, ×4.5, U.S.N.M. 137105b. *39*, paratype, free cheek with broken genal spine, ×5, U.S.N.M. 137105e. *42,35*, holotype, dorsal and profile views of small cranidium with well-preserved outer surface, ×7, U.S.N.M. 137104. *36,43*, paratype, dorsal and profile views of largest pygidium broken but showing the granules on pleural platforms and wrinkles on axis and border, ×3, U.S.N.M. 137105f. *41*, paratype, meraspid pygidium, ×10, U.S.N.M. 137105g. *37,38,40*, paratypes, small holaspid pygidia, ×8, ×4, ×7.5, U.S.N.M. 137105d, U.S.N.M. 137105i, U.S.N.M. 137105h.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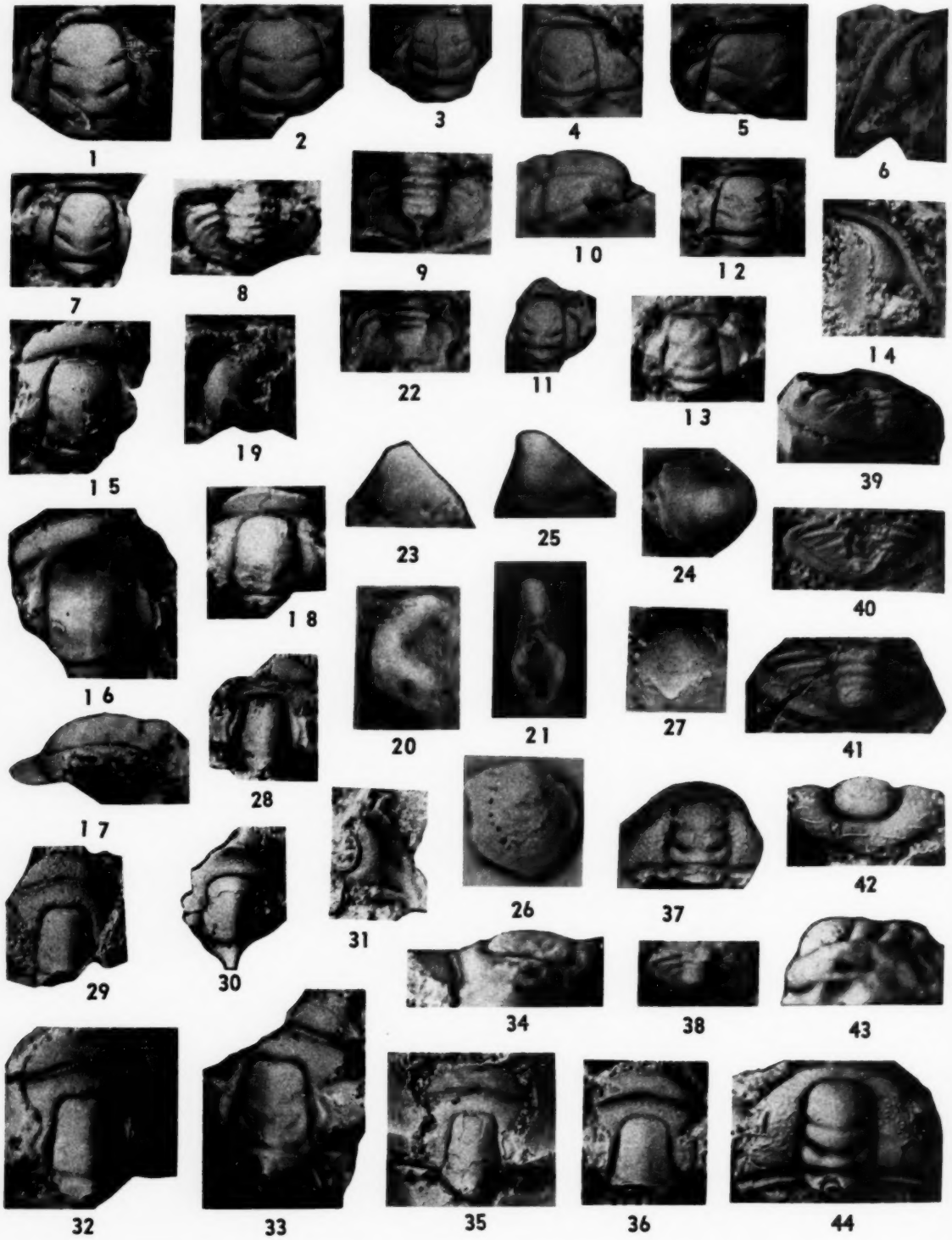
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MEERIA Frederickson 1949
subgenus of IDAHOIA

Supplementary description: Free cheek rectangular, with short genal spine; lateral and posterior border furrows separated at genal angle by low swell.

Pygidium narrow-transverse, axis wide, convex, with broad post-axial ridge, 3 axial rings and terminal portion, pleural platform narrower than axis, moderately downsloping into the medium-width, concave border, interpleural grooves broad and deep, curving posteriorly onto the border, pleural furrows faint, border furrow obsolete.

Outer surface with very fine granules and/or a bertillon pattern of low wrinkles and ridges; inner surface apparently smooth.

Remarks: At the time *Meeria* was described it was known only from the cranidia of the genotype, *M. lirae*, none of which was particularly well preserved. Subsequently specimens of another species from Texas and the species here described as *I.* (*Meeria*) *modesta*, n. sp. have added greatly to our knowledge of this group, and demonstrate its very close relation to the species placed in *Idahoia* (s.s.). Free cheeks and pygidia are associated with the cranidia of the Idaho species and their description has been added above.

The group of species placed in *Meeria* differs consistently from the generic concept of *Idahoia* (s.s.) in a few minor features of the cranidium and pygidium:—1) the stronger convexity of the glabella which gives the glabella the appearance of being shorter, although proportional measurements indicate it is not; the more distinct glabellar furrows; and the absence of an occipital spine. 2) on the pygidium the axis appears somewhat wider and more convex, and the border narrower than in the typical *Idahoia*. None of these features in itself has

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EXPLANATION OF PLATE 60

FIGS. *1–14—Drumaspis walcotti* Resser. *1,7*, two small peeled cranidia, ×6, ×5, U.S.N.M. 137106a, 137106h. *12*, small nearly complete cranidium, ×5.5, U.S.N.M. 137106k. *11,13*, smallest cranidia, with some of outer surface, ×5, ×10, U.S.N.M. 137106m, 137106L. *2,3*, two broken medium-sized cranidia, ×2.6, ×3, U.S.N.M. 137106b, 137106c. *5*, fragment of largest cranidium, about 12 mm complete, ×3, U.S.N.M. 137106g, *4,10*, dorsal and profile of small cranidium with granules of the outer surface, ×6, U.S.N.M. 137106d. *6,14*, two free cheeks with outer surface, ×2.5, ×4, U.S.N.M. 137106i, 137106j. *8*, plesiotype, pygidium with weathered outer surface, ×5, U.S.N.M. 137106o. *9*, plesiotype, pygidium with good outer surface on pleural regions, ×5, U.S.N.M. 137106n.

15–18—Wilbernia pero (Walcott). *15*, medium-sized, weathered cranidium, ×2.5, U.S.N.M. 137107a. *16,17*, dorsal and profile of largest cranidium, ×1, U.S.N.M. 137107c, *18*, smallest cranidium with some of outer surface, ×4, U.S.N.M. 137107b.

19–21—Pelagiella sp. undet. *19*, limestone mold with broken apex, ×5, U.S.N.M. 137108a. *20,21*, side and dorsum of one of etched steinkerns, ×5, U.S.N.M. 137108b.

22—pygidium, gen. and sp. undet. dorsal view of small pygidium which cannot be associated with a cranidium, ×9, U.S.N.M. 137111.

23–25—cf. *Acrotreta* sp. undet. anterior, apical and profile views of only specimen, ×25, U.S.N.M. 137109.

26,27—Obulus sp. undet. *26*, larger weathered valve, ×8.5, U.S.N.M. 137110a. *27*, smaller valve with growth ridges and fine costellae, ×20, U.S.N.M. 137110b.

28–36—Idahoia serapio Walcott. *28*, cranidium with some outer surface—granules along anterior border are on inner surface only, ×2.5, U.S.N.M. 137112a. *29*, cranidium with weathered inner surface showing granules and glabellar furrows, ×2, U.S.N.M. 137112c. *30*, small cranidium with some of outer surface and occipital spine, ×4, U.S.N.M. 137112d. *31*, free cheek with well-preserved outer surface, ×3.8, U.S.N.M. 137112b. *32–34*, dorsal, front and profile of medium-sized cranidium with glabellar furrows, ×1.7, U.S.N.M. 137112e. *35,36*, two medium-sized cranidia, ×3, ×2.8, U.S.N.M. 137112f, U.S.N.M. 137112g.

37–44—Ptychaspis granulosa Owen. *37*, smallest pygidium with good outer surface, ×5, U.S.N.M. 137113e. *39*, largest pygidium, ×2, U.S.N.M. 137113c. *40,41*, two small, more complete pygidia, ×4, U.S.N.M. 137113f, U.S.N.M. 137113d. *42–44*, side, front and dorsal of medium-sized cranidium, ×2, U.S.N.M. 137113a. *38*, small, distorted cranidium, ×3, U.S.N.M. 137113b.

more than specific value, yet the combination of them results in a form which cannot be readily placed in *Idahoia* (s.s.). The recognition of *Meeria* as a subgenus seems to best express the relationship of the two groups.

Meeria is similar to *Idahoia* (s.s) in all structural features of the cranidium and pygidium, with the exception of the few details mentioned above. The ornamentation of the outer surface is also the same, but the known cranidia of *Meeria* show no row of granules along the anterior border furrow on the inner surface as in *Idahoia* (s.s.). The morphology of the exoskeleton of the *Meeria* species suggests a trend toward more primitive ptychoparoid structures. In Oklahoma *Meeria* appears in a faunule at the top of the *Conaspis* faunizone; the undescribed species from Texas occurs in a faunule at the base of the *Ptychaspis* subzone; and *Meeria modesta* in Idaho is in the upper part of the *Ptychaspis* subzone. The Idaho species occupies the highest known stratigraphic position of *Meeria*, and may indicate the upper limit of the biozone of the subgenus.

Idahoia (Meeria) modesta, n. sp.
Pl. 59, figs. 33–45

Cranidium with convex, truncato-conical glabella (width at base (tr) equals length (sag)), front straight, three pairs of shallow glabellar furrows, dorsal furrow distinct, occipital furrow broad, occipital ring with small median node, preglabellar field convex, downsloping, anterior furrow distinct, anterior border convex, crescentic; fixed cheek—anterior area narrow, downsloping, anterior facial suture diverging slightly to furrow, then curving in across anterior border, palpebral area low, slightly upsloping, $\frac{1}{3}$ glabellar width, faint eye ridge, palpebral lobe medium size, opposite center of glabella, posterior area narrow, $\frac{2}{3}$ length (tr) of occipital ring. Free cheek rectangular with short genal spine, ocular platform convex, downsloping, lateral furrow distinct but ends before reaching posterior furrow, narrow convex lateral border.

Pygidium transverse, axis strongly convex, wider than pleural platforms, extending $\frac{4}{5}$ length of pygidium with broad, post axial ridge to margin, 3 axial rings and terminal portion, dorsal furrow shallow, at sides only, pleural platform slightly downsloping into narrow concave border, 3 pleurae, interpleural grooves broad, distinct, curved posteriorly onto border, pleural furrows shallow, border furrow obsolete.

Outer surface with close, fine granules and low irregular ridges on axial portions of exoskeleton, narrow ridges paralleling the margins on genal spine, the lateral, anterior and posterior borders; inner surface apparently smooth.

Remarks: Fifteen cranidia, several free cheeks and four small pygidia have been referred to this species. The cranidia range in size from 2 mm. to 13 mm. in length and the pygidia .75 mm. to 1.5 mm. in length.

Cranidia with the outer surface well preserved show very fine granules on the glabella and palpebral areas and preglabellar field, and irregular wrinkles on the anterior border. The holotype is the only cranidium with a perfect outer surface, but several other small cranidia have portions of the granulated surface preserved. On the pygidia the fine granules cover the axis and pleural platforms and the "bertillon" pattern of fine wrinkles appears on the posterior end of the axis and over the border.

Types: holotype, cranidium, U.S.N.M. 137104; paratypes, cranidia, U.S.N.M. 137105a-c; paratypes, free cheeks, U.S.N.M. 137105e; paratypes, pygidia, U.S.N.M. 137105d,f-i

Saratogia Walcott 1916 vs. Idahoia Walcott 1925

The two genera, *Idahoia* and *Saratogia*, are very similar, a number of species have been shifted from one genus to the other during the years, and there has never been given any clear statement of the generic features upon which they can be separated. Walcott established the genus *Saratogia* in 1916 with *S. calcifera* (Walcott) as the genotype, from the Hoyt limestone of New York, and assigned to the genus also *S. hamulus* (Owen), *S. wisconsensis* (Owen) and *S. hera* Walcott, all from the Franconian of Wisconsin and Minnesota. In 1925 Walcott established *Idahoia* with the genotype *I. serapio* Walcott from the St. Charles formation and stated "*Idahoia*, during its study, was first

regarded as a relative of *Saratogia*, but the absence of glabellar and occipital furrows, the wider fixed cheeks, the intramarginal suture and the frontal limb give the genus very distinctive characters." Walcott erred in overemphasizing certain of these features.

In 1935 Resser placed the four Upper Mississippi valley species of *Conocephalites wisconensis* (Owen), *Conocephalites latifrons* (Shumard), *Conocephalites hamulus* (Owen), and *Saratogia hera* Walcott in the genus *Idahoia*, without commenting upon the reasons for the change or giving his opinion on the relationship between the genera *Idahoia* and *Saratogia*. In 1952 Bell, Feniak and Kurtz recognized specimens of *I. wisconensis* (Owen), *I. hamulus* (Owen) and *I. hera* (Walcott). The original types of *I. latifrons* (Shumard) have long been lost, and the fragmentary cranidium figured by Hall and referred to by Resser is too poor for accurate generic determination since only the anterior portion of the glabella and the frontal area are present. The specimen must be regarded as unrecognizable.

In 1950 Lochman gave a diagnosis of *Idahoia* in discussing the distinctions between *Idahoia* and *Wilbernia*. This diagnosis in greater detail is repeated here for comparison with a diagnosis of *Saratogia*.

Diagnosis of Idahoia

Cranidium: 1) palpebral lobes medium size, crescentiform, wide, opposite, or very slightly anterior or posterior to center of glabella. 2) glabella broadly conical with nearly straight front; convexity regular, fairly low; two or three pairs of faint glabellar furrows. 3) fixed cheek—palpebral area less than one-half, not quite one-third glabellar width, measured with palpebral lobes. 4) palpebral area flat, horizontal. 5) posterior area narrow, two-thirds length (tr) of occipital ring. 6) row of granules at posterior edge of anterior border furrow on inner surface only.

Pygidium: 1) broadly ovate; axis convex, of medium width, tapered. 2) border wide, variable in slope, often concave.

Diagnosis of Saratogia

Cranidium: 1) palpebral lobes medium size, crescentiform, wide, opposite or very slightly posterior to center of glabella. 2) glabella broadly conical with nearly straight front; convexity regular, low; three pairs of faint glabellar furrows. 3) fixed cheek—palpebral area less than one-half, not quite one-third glabellar width, measured with palpebral lobes. 4) palpebral area flat, horizontal. 5) posterior area narrow, about one-half length (tr) of occipital ring. 6) row of small granules in anterior border furrow on inner surface only.

Pygidium: 1) narrow- transverse, strongly convex, axis convex, of medium width, tapered. 2) border very narrow, downsloping.

The external ornamentation of the exoskeleton is the same in both genera.

The diagnoses indicate that there are no truly significant generic distinctions between the cranidia of *Idahoia* and *Saratogia*. Four of the features mentioned by Walcott are the same in both genera—both show faint glabellar furrows, an occipital furrow, the same width of the palpebral area, and an intramarginal facial suture. The only consistent distinctions which can be detected in the cranidia are 1) the apparent lesser length of the posterior area in *Saratogia*, 2) the narrower (tr) anterior area of the fixed cheek, and 3) the convexity of the frontal area (frontal limb of Walcott). In *Idahoia* the course of the anterior facial suture varies from widely divergent (in *I. serapio* and *I. wisconsensis*) to nearly straight forward (in *I. hamulus*), and the frontal area has a low convexity or is flat, with the anterior border either horizontal or downsloping. In *Saratogia calcifera* and *S. fria*, n. sp. the anterior facial suture diverges only slightly, the preglabellar field continues the steep downslope of the front of the glabella and the anterior border is strongly convex, and may even appear somewhat upturned. The pygidium which has been associated with *S. calcifera* is markedly different from that of *Idahoia*, and if the association can be substantiated would certainly justify keeping the genera distinct. No pygidia can be associated with the new species from Idaho, so both genera are still recognized.

The two genera are closely related. The longer range of *Saratogia* into the *Saukia* zone suggests that it may be a specialized end form resulting from one of the *Idahoia* species with a narrow frontal area.

SARATOGIA FRIA n. sp.
Pl. 59, figs. 1–11

Cranidium rectangular, glabella truncato-conical, low convexity, three pairs of faint glabellar furrows, anterior straight, posterior two pairs diagonal, dorsal furrow shallow, occipital furrow wide, shallow, occipital ring broad with a flat, medium-length spine, and a small median node; preglabellar field ½ the glabellar length (sag), convex and downsloping, anterior furrow wide, shallow, anterior border one-half width (sag) of preglabellar field, convex, horizontal; fixed cheek—palpebral area one-third glabellar width, slightly convex and downsloping, anterior facial suture running nearly straight forward, palpebral lobe medium-size, a little posterior to center of glabella, palpebral furrow shallow, eye ridge distinct, posterior area narrow, length unknown. Free cheek with long genal spine; ocular platform wide, convex, lateral furrow wide and shallow, border medium width, strongly convex. Pygidium unknown.

Outer surface of test not known; inner surface of glabella smooth, caecal venations on preglabellar field and ocular platform, a row of granules on the anterior furrow (20–22), anterior border may have fine punctae.

Remarks: About 20 cranidia and four free cheeks have been assigned to this species—the cranidia ranging in size from 2 mm. to 16 mm. in length (excluding the occipital spine). This species differs from *Saratogia calcifera* cranidia in only two minor features—1) the apparently slightly greater width (tr) of the anterior area of the fixed cheeks, and 2) the position of the palpebral lobes very slightly posterior to the center of the glabella. The convexity and slope of the preglabellar field and the anterior border are the same in the two species. There are no distinguishable differences in the associated free cheeks, but no pygidium similar to that associated with *S. calcifera* has been noted in this material.

Types: holotype, cranidium, U.S.N.M. 137102; paratypes, cranidia, U.S.N.M. 137103a-e,h,k; paratypes, free cheeks, U.S.N.M. 137103f,g.

Genus WILBERNIA Walcott, 1924
WILBERNIA PERO (Walcott)
Pl. 60, figs. 15–18

Ptychoparia pero WALCOTT, 1890, p. 274, pl. 21, fig. 6.
Anomocare pero (Walcott) WALCOTT, 1912, p. 212.
Wilbernia pero (Walcott) WALCOTT, 1924, p. 60, pl. 13, fig. 4; NELSON, 1951, p. 782, pl. 109, fig. 13 (synonymy to date).
Wilbernia cf. *pero* (Walcott) BELL, FENIAK & KURZ, 1952, p. 195, pl. 34, figs. 5a–c.

Eight cranidia ranging in size from 2.5 mm. to 26 mm. in length have been referred to this species. All are in the holaspid stage and most are well preserved though fragmentary. The row of granules in the anterior border furrow is well preserved, and those specimens with the outer surface show a very distinctive "bertillon" pattern of narrow ridges, especially on the glabella and anterior border. These specimens show that in the smaller holaspid cranidia the glabella is still slightly conical, whereas in the largest cranidia it is distinctly quadrate with parallel sides.

Figured specimens: cranidia, U.S.N.M. 137107a-c.

Family PTYCHASPIDIDAE
PTYCHASPIS Hall, 1863
PTYCHASPIS BULLASA, n. sp.
Pl. 58, figs. 21-42

Cranidium trapezoidal in outline; glabella nearly parallel-sided, front rounded, convexity low, rising slightly above the fixed cheeks, two pairs of glabellar furrows, deeply impressed at sides, shallow across center; occipital ring convex, with small median node; occipital furrow broad and deep; frontal area one-sixth length (sag) of glabella, posterior half only slightly downsloping, anterior half in front of a prominent transverse ridge, vertical, anterior margin bluntly pointed; fixed cheek—palpebral area horizontal, slightly convex, over half width of glabella, palpebral lobe small, opposite anterior third of glabella, posterior area wide (ex sag), triangular, same length (tr) as occipital ring. Free cheek narrow, elongate, with broad-based genal spine; ocular platform convex; lateral and posterior furrows deep, joining at an acute angle, lateral border convex. Hypostoma narrow, elongate, strongly convex; posterior lobe convex, crescentic, marginal furrow distinct; central lobe bounded at sides by curved furrow, deep posteriorly, shallowing

anteriorly; facet area flat, triangular.

Pygidium narrowly transverse; axis moderately convex, sides tapered slightly to broadly rounded end, shallow dorsal furrow; 3 axial rings and terminal portion; pleural regions wider than axis, convexity low, three pleural segments separated by broad interpleural grooves and crossed by narrow, distinct pleural furrows; marginal furrow broad, shallow; border narrow, upturned to vertical position.

Outer surface—coarse granules on glabella and fixed cheeks, furrows smooth, two short curved ridges at each side on anterior area of fixed cheeks; frontal area crossed by one or two narrow transverse ridges; free cheek—ocular platform with coarse granules and several narrow imbricating ridges, lateral border with two ridges anteriorly, increasing posteriorly to six or more on genal spine; pygidium possibly with fine granules. Inner surface of exoskeleton with punctae of two sizes.

Remarks: This species is represented by over 80 specimens (about 40 cranidia, 20 free cheeks and 20 pygidia). The cranidia range in size from .7 mm. to 20 mm. in length and the pygidia from .3 to 7 mm., thereby enabling us to work out a growth series from the late meraspid stage through the large holaspid. The meraspid cranidium is rectangular in outline with a narrow conical glabella tapering anteriorly; the two pairs of glabellar furrows are already distinct but are placed within the posterior half of the glabella due to the greater length of the anterior half which is low and nearly flat; and there is a distinct median node on the occipital ring. Most interesting is the position of the proportionately larger palpebral lobes opposite the center of the glabella, recapitulating the position found in the ancestral forms—*Eoptychaspis* and *Ptychaspis arcolensis* Nelson. On cranidia of the early holaspid molts (1 mm. to 3 mm.) the glabella begins to assume a truncato-conical shape, but is still more convex posteriorly than anteriorly; the palpebral lobes are still large and opposite the center of glabella. With continued growth (at 6 mm. in length) the glabella becomes parallel-sided, shorter and wider, and the anterior lobe more convex; and the palpebral lobe becomes proportionately smaller and moves into its anterior position. The coarse granules on the outer surface are already present in the meraspid stage.

Two meraspid pygidia (2½ mm. and 3½ mm. in length) retain several of the thoracic segments. The smallest pygidium retains fragments of four thoracic segments anterior to the pygidium, which shows three axial rings and terminal portion. On the pleural regions, although the segments are fused, the falcate terminations of the separate segments are not yet resorbed and appear along the posterior border as four pairs of very tiny marginal spines. In the larger meraspid pygidium two thoracic segments occur with the pygidium, which also has 3 axial rings and terminal portion; but the shape is more transverse and the falcate terminations of the pleural segments are nearly resorbed, leaving four pairs of low arcs along the posterior margin.

The cranidium of *P. bullasa* is most similar to that of *P. granulosa* (Owen). The glabella has the same shape and convexity but instead of being depressed between the fixed cheeks as in *P. granulosa*, it stands above the low horizontal fixed cheeks; the frontal area of *P. bullasa* is proportionately longer (sag) than that of *P. granulosa* and the posterior half is only slightly downsloping whereas in *P. granulosa* the entire frontal area is nearly vertical in position. The pygidium which we have associated with *P. bullasa* because of the larger number of specimens is quite unlike that associated with *P. granulosa* but very similar to that associated with *P. tuberosa* Kurz from the *P. striata* subzone of Wisconsin. The pygidia have the same axial shape and the same sharply upturned border, but the outline of *P. bullasa* appears to be more narrowly transverse. Nearly all the replica specimens have the border broken off in the reverse impression, so that only the relatively flat portion immediately behind the axis is complete and shows the posterior margin. The outer surface of these pygidia is not well preserved, but appears to have been granular.

Types: holotype—cranidium, U.S.N.M. 137099; paratypes—cranidia, U.S.N.M. 137100a-e,i,k,r,n; free cheeks, U.S.N.M. 137100j,f,g; pygidia, U.S.N.M. 137100

L,o,p,h,s; hypostome, U.S.N.M. 137100m; thoracic pleuron, U.S.N.M. 137100t.

PTYCHASPIS GRANULOSA (Owen)
Pl. 60, figs. 37–44

Dikelocephalus granulosus OWEN, 1852, p. 575, table 1, fig. 5,7.
Ptychaspis granulosa (Owen) WHITFIELD, 1878, p. 54; 1882, p. 185, pl. 1, fig. 24. BELL, FENIAK & KURTZ, 1952, p. 193, pl. 34, figs. 6a,b, pl. 35, figs. 1a–e (synonymy to date).

Remarks: About twenty-eight cranidia and eighteen pygidia are referred to this species. The form is noticeably less abundant in the material than *P. bullasa*, n. sp. The cranidia are coarsely granular and have been distinguished from *P. bullasa* by the sunken position of the glabella and the essentially vertical position of the preglabellar field which cannot be seen from the dorsal view. Although the two species of *P. bullasa* and *P. granulosa* can be separated on these features in the cranidium, sharper distinctions exist in respect to the pygidia. In this respect *Ptychaspis* is reminiscent of certain genera of the Dolichometopidae which show little appreciable variation in the cephalon. In *P. granulosa* the parallel-sided glabella may not be always definitely sunken below the fixed cheeks, and the preglabellar field may be steeply sloping rather than vertical. Both changes are shifts toward characteristic features of *P. bullasa*, and on the basis of the cephalon alone it could be argued that the two species represent end members of a gradational series.

The pygidium of *P. granulosa* is distinguished by its gently sloping pleural platform and narrow almost flat border. In spite of the coarsely granular surface of the cranidum, no granules have ever been reported from associated pygidia. The pygidia here associated with *P. granulosa* cranidia have the outer surface well preserved and show a surface ornamentation of medium-sized imbricating ridges which are quite prominent on the border. It is suspected that these imbricating ridges were the common surface ornamentation over the pygidium and thorax of all species of *Ptychaspis*, and that only in a few species did they break up to form rows of coarse granules on the cranidium and inner part of free cheek. The free cheeks of several species show the transition from ridges to granules.

Figured specimens: cranidia, U.S.N.M. 137113a,b; pygidia, U.S.N.M. 137113c-f

INCERTAE SEDIS
TAENICEPHALINA GLOBULA, n. sp.
Pl. 57, figs. 34–43

Cranidium quadrate, convex; glabella broadly conical, front rounded, moderately convex, broad deep dorsal furrow, three pairs of glabellar furrows distinct on interior, faint on exterior, anterior pair straight, posterior pairs curved, occipital furrow deep, occipital ring convex with small median node; preglabellar field about $\frac{1}{3}$ length (sag) of glabella, convex, downsloping, anterior border furrow straight, shallow at sides, deep across middle, anterior border flat, subtriangular, continuing steep downslope of front of preglabellar field-fixed cheek—anterior area wide, downsloping, anterior facial suture running straight forward, then curving inward at border furrow, palpebral area convex, horizontal, somewhat less than one-half glabellar width, palpebral lobe small, anterior to center of glabella, eye ridge narrow, distinct, palpebral furrow broad, posterior area wide (ex sag), convex, $\frac{3}{4}$ length (tr) of occipital ring. Free cheek not known.

Pygidium small, transverse, convex; axis wide, strongly convex, tapered only slightly $\frac{3}{4}$ length, continuing to margin as a broad post axial ridge, 2 axial rings and terminal portion with narrow 3rd ring, pleural regions narrower than axis, steeply downsloping to margins, 2 pleurae separated by broad interpleural grooves, pleural furrows faint, border furrow obsolete, narrow convex border, posterior margin with broad median inbend.

Inner surface punctate with caecal venations on preglabellar field; one specimen also showing widely scattered, medium-sized granules on fixed cheeks and preglabellar field; outer surface very finely granular with a few medium-sized granules on cranidium, several narrow parallel ridges on each side of the anterior border.

Remarks: Fifteen small cranidia and one small pygidium have been referred to this species. The cranidia range from 2 mm. to 5 mm. in length (sag) and the pygidium is only 1 mm. The cranidia are rather close

to those of *Taenicephalina lechevalieri* Rasetti, the genotype and only other known species of the genus. Among the Idaho specimens there is the same variation in shape of the glabella from conical to broad-conical.

T. globula differs from the genotype in the more distinct glabellar furrows on the inner surface, the slightly narrower (sag) preglabellar field and the steeply downsloping position of the anterior border. Although Rasetti states in his description of the genus that the small palpebral lobes are "opposite the glabellar midpoint," his photographs show them as somewhat anterior to the center of the glabella.

Types: holotype, cranidium, U.S.N.M. 137093; paratypes, cranidia, U.S.N.M. 137094a-c, e-g; paratype, pygidium, U.S.N.M. 137094d.

Phylum GASTROPODA
Suborder BELLEROPHONTACEA
Family SINUITIDAE
ANCONOCHILUS IDAHOENSIS, n. sp.
Pl. 57, figs. 25–33

Small, involute, narrowly phaneromphalus shells with a broad V-shaped sinus at anterior lip; dorsum of whorl section broadly curved, sides of dorsal slope flattening in steinkern, but on outer surface curvature continues to an obtuse angle with the ventral slope; umbilicus apparently open; on exterior a distinct narrow slit band running along center of dorsum interrupting the low arcuate growth ridges which parallel the sides of the apertural sinus.

Remarks: Over fifty specimens, many of them steinkerns, but a few showing the exterior surface markings have been obtained. All the shells are small, the average 2 mm. across the whorls, the largest 3 mm. It can be assumed that the shells belonged to rather young specimens, and this makes a positive generic and specific identification difficult. *Sinuella* Knight is a small gastropod described from the basal Franconian beds of Texas which in general appearance is quite similar to these specimens, but it is characterized by an unusual concave dorsum which is readily seen even on steinkerns. *Owenella* is a rather common form in the Trempealeauan, but it differs both in shape and surface ornamentation from the Idaho specimens. The specimens of *Anconochilus barnesi*, genotype and only described species, are much larger than these specimens but they do show the same kind of apertural sinus, the same rounded dorsum, the probable open umbilicus and same shell shape. Under these circumstances, *Anconochilus* appears the best generic assignment of the species.

Types: Holotype, U.S.N.M. 137091; paratypes, U.S.N.M. 137092a–g.

Subclass PROTOGASTROPODA
Order COCHLIOSTRACA
PELAGIELLA sp. undet.
Pl. 60, figs. 19–21

The material which was etched furnished a number of steinkerns of an open, slightly asymmetrically coiled snail shell which appears to be referable to *Pelagiella*. Only one limestone mold with a broken apex has been recovered and this adds nothing further concerning the form. Specimens showing the two kinds of preservation have been figured for reference.

Figured specimens: steinkern, U.S.N.M. 137108b; limestone mold, U.S.N.M. 137108a

Phylum BRACHIOPODA
Order ATREMATA
Family OBOLIDAE
OBOLUS sp. undet.
Pl. 60, figs. 26,27

Two small valves referable to *Obolus* have been obtained. The larger has lost nearly all the calcareo-phosphatic shell and is mainly a limestone mold, while the smaller has a well preserved shell showing the concentric growth lines and very fine radiating costellae. Many fragments of calcareo-phosphatic shells were found in the etched material. These probably belong to either *Obolus* or the acrotretid genus, but their fragmentary condition prevents accurate identification. The fragmentary condition indicates that the brachiopods, like most of the trilobites in the material, were deposited in the debris piles rather than actually living upon them.

Figured specimens: two shells, U.S.N.M. 137110a,b

Order NEOTREMATA
Family ACROTRETIDAE
cf. ACROTRETA sp.
Pl. 60, figs. 23–25

A single ventral valve of an Acrotretid type shell was obtained from the material. The exterior shell is well preserved and the valve appears to be complete, but there is no way of determining the internal markings on the single specimen so that more exact generic determination cannot be made until additional specimens have been obtained.

Figured specimen: ventral valve, U.S.N.M. 137109

Suborder ORTHOIDEA
Family BILLINGSELLIDAE
BILLINGSELLA cf. B. PLICATELLA Walcott
Pl. 57, figs. 17–20

Remarks: A species of *Billingsella* is represented by three limestone replicas and a number of fragmentary silicified shells. One valve is essentially complete with a well preserved exterior. In external appearance the valves closely resemble *B. plicatella* which occurs in association with the faunules of the *Ptychaspis-Prosaukia* faunizone in the Snowy Range formation of southern Montana and northern Wyoming.

The surface of the valve is crossed by 33 to 35 costellae, all of about the same size on comparative parts of the valve, and increasing by implantation; concentric growth lines very numerous, fine, with three or four much thickened lines where growth was interrupted for a time; the numerous fine growth lines crossing the low rounded costellae give the surface a reticulate appearance. There is no distinct fold or sulcus, and the valve is widest opposite the center, with the line of commissure curving inward to the shorter hinge line. The valve appears to have a low regular convexity, but the anterior margin is now somewhat crushed. On none of the valves is there any indication of the internal structures which are necessary for accurate identification of the species.

One of the specimens is an immature valve, measuring 5.5 mm. in length×6.25 across the hinge line. Two other valves may be considered near adult size, measuring 15 mm. in width through the middle of the valve, 14 mm. in width at the hinge line and 14 mm. in length.

Figured specimens: U.S.N.M. 137090a–d

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THE GASTROPOD GENUS *CERATOSTOMA*

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ABSTRACT—The species belonging to the genus *Ceratostoma* are listed and some are figured, as are forms that closely resemble the genus. The genus is characterized by three varices, foliations on the varices, and a tooth on the anterior portion of the outer lip. The genus *Ceratostoma* lives in a littoral marine environment with water temperatures ranging from 2 to 27 degrees Centigrade. Known time range of the genus is from the Middle Miocene to the Recent.

INTRODUCTION

THE genus *Ceratostoma* was first recognized in 1784 by Martyn, under the name *Purpura*. The International Commission on Zoological Nomenclature in Opinion 456, dated 15 March 1957, has rejected Martyn's work as not available. Hence an alternative name—*Ceratostoma*—for this distinctive gastropod group has been employed and most of the species that comprise the genus are listed.

As some paleontologists and malacologists have confused the genera *Pterorhytis*, *Pterynotus*, and *Ocinebrellus* with *Ceratostoma*, they are figured here with fossil and living species of *Ceratostoma* in order to clearly show differences.

This shallow water genus has certain characteristics that are always common to the species, but there are striking differences between two taxa—these two may constitute separate subgenera. One subgenus would include *C. nuttalli*, *C. fournieri*, *C. rorifluum*, and *C. monoceros;* and the other would include *C. foliatum*, *C. burnetti*, *C. delorae*, *C. nanna*, *C. perangulatum*, *C. turris*, *C. plorator*, and *C. esychus*. Several members of the first group mentioned can tolerate water no colder than 13 or 14°C., the latter water as cold as 2°C. and no warmer than 19°C.

SYNONYMY

In 1837, Conrad (p. 263) published the generic name *Cerostoma*, the type species by monotypy being *Cerostoma nuttalli*. However, *Cerostoma* must be rejected under the Law of Homonymy in favor of *Cerostoma* Latreille (1802, p. 416), which is an insect Herrmannsen (1846, p. 206), emended the name *Cerastoma* Conrad—under the mistaken impression that this was Conrad's spelling—to *Ceratostoma* in a nomenclator as follows: "*Rectius Ceratostoma vel Cerostoma.*" *Cerastoma* cannot be recognized as an emendation, for that name is also preoccupied (Koch, 1839, p. 29).

In a petition before the International Commission of Zoological Nomenclature I have asked:

1) To validate the generic name *Ceratostoma* Herrmannsen, 1846, even though that name was published in a nomenclatorial index.

2) To place the name *Ceratostoma* on the Official List of Generic Names in Zoology.

3) To place the under-mentioned name on the Official List of Specific Names in Zoology:

nuttalli Conrad, 1837. The type species (by monotypy) of the genus *Ceratostoma*.

4) To place the under-mentioned generic names on the Official Index of Rejected and Invalid Generic Names in Zoology:

a) *Cerostoma* Conrad, 1837 [a homonym of *Cerostoma* Latreille (1802), Insecta].

b) *Cerastoma* Herrmannsen, 1846 (an erroneous subsequent spelling of *Cerostoma*) [a homonym of *Cerastoma* Koch (1839), Arachnida].

SYSTEMATICS

Family MURICIDAE

Genus CERATOSTOMA Herrmannsen, 1846

"*Purpura* Martyn, 1784" of authors (non-binomial).

Cerostoma Conrad, 1837, p. 263, (not *Cerostoma* Latreille, 1802, p. 416, Insecta).
Ceratostoma Herrmannsen, 1846, p. 206 (emendation of *Cerastoma*, spelling error for *Cerostoma*).

Type.—*Cerostoma nuttalli* Conrad, 1837, by monotypy.

The genus is characterized by three varices (except in *C. rorifluum*, which has four), foliations on the varices, and a tooth on the anterior portion of outer lip.

CERATOSTOMA NUTTALLI (Conrad, 1837)
Pl. 1, figs. 1,2,8; 3,4,12

Murex (*Cerostoma*) *nutalli*, Conrad, 1837, p. 264, pl. 20, fig. 22.
Murex nuttalli Conrad, Sowerby, 1880, p. 27.
Cerostoma nuttalli Conrad, Cooper, 1888, p. 233.
Murex (*Pterorhytis*) *nuttalli* Conrad, Arnold, 1903, p. 245.
Purpura nuttalli albescens Dall, 1919, p. 332; 1921, p. 107; Oldroyd, 1927, p. 14.
Purpura nuttalli Dall, 1921, p. 107; Jordan, 1926, p. 245; Grant and Gale, 1931, p. 705.

Hypotype.—Univ. of Calif. at Los Angeles Cat. Nos. 28994 and 28995.

Type locality.—Santa Barbara, California, Recent. (Type specimen at the Acad. Nat. Sci. Philad.).

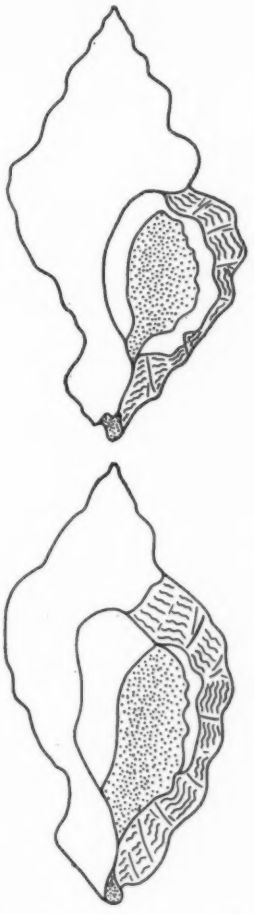
Distribution.—Pleistocene: Rare in Pleistocene fauna at Deadman Island; Pleistocene at San Quintin Bay, Lower Calif. Mexico.

Recent: Scammon's Lagoon, Lower California, to Montery Bay, Calif. (27 to 37 degrees Latitude). Living in water with an approximate temperature of 13 to 22 degrees Centigrade. This is a shallow water or littoral form living at depths of between 0 and 20 fathoms.

Remarks.—Commonly not as frilled as *C. foliatum*, and with teeth on inside of outer lip. *C. nuttalli* has a smaller thorn-like tooth on outer lip than *C. monoceros*, *C. monoceras* slightly higher spired than *C. nuttalli*, and with a more distinct shoulder (see Text-fig. 1).

CERATOSTOMA MONOCEROS (Sowerby, 1841)
Pl. 2, figs. 4–6

Murex monoceros Sowerby, 1841, p. 143; 1841, p. 5, figs. 64,65; Kiener, p. 28, pl. 10, fig. 86. [Not *Murex monoceros* d'Orbigny, p. 454, pl. 78, figs. 1,2.]
Murex (*Cerostoma*) *monoceros* Sowerby, Tryon, 1880, p. 115, pl. 35, figs. 388,389.
Murex (*Pterorhytis*) *monoceros* Sowerby, Arnold, 1903, p. 246.



TEXT-FIG. *1*—Differences in outline between *Ceratostoma monoceros* (top) and *C. nuttalli* (bottom).

Purpura monoceros Sowerby, Stewart, 1927, p. 388, pl. 32, fig. 1.

Hypotype.—Calif. Acad. Sci. Dept. Paleo. type coll. no. 9507.

Type locality.—Lower California, Mexico, Recent.

Distribution.—Pleistocene: Santa Barbara formation; San Pedro formation; San Diego formation.

Recent: Lower California, Mexico. Living in water between 14 and 24 degrees Centigrade.

CERATOSTOMA FOURNIERI (Crosse, 1861)
Pl. 1, figs. 5–7

Murex fournieri Crosse, 1861, p. 352, pl. 16, fig. 7.

Hypotype.—Stanford Univ. Paleo. Type Coll. no. 8493.

Type locality.—Japanese waters 13–27°C. Recent.

CERATOSTOMA RORIFLUUM (Adams & Reeve, 1850)
Pl. 1, figs. 9–11

Murex rorifluus Adams & Reeve, p. 38.
Murex monachus Crosse, 1862, p. 55. pl. 1, fig. 9.

Hypotype.—Stanford Univ. Paleo. Type Coll. No. 8494.

Type locality.—Japanese waters 6–27°C.; Recent.

Remarks.—Weak tooth, more clearly seen on older varices, smoother shell than *C. nuttalli*, 4 varices.

CERATOSTOMA FOLIATUM (Gmelin, 1791)
Pl. 1, figs. 13–15;Pl. 4,5,7

Purpura foliata Martyn, 1784, pl. 66 (non-binomial); Dall, 1921, p. 106; Oldroyd, 1927, p. 14; Grant & Gale, 1931, p. 705.
Murex foliatus Gmelin, 1791, p. 3529; Reeve, 1845, pl. 3, fig. 12.
Murex foliatus Martyn, Sowerby, 1880, p. 24, pl. 11, fig. 110.
Murex (Cerostoma) foliatus Martyn, Tryon, 1880, p. 113, pl. 34, figs. 370,371.
Murex (Pterorhytis) foliatus Martyn, Arnold, 1903, p. 245.
Murex phyllopterus Lamarck, Sowerby, 1834; 1880, p. 24, fig. 107.
Purpura perponderosa Dall, 1922, p. 46, pl. 2, figs. 2,5; Howe, 1922, p. 93.

Hypotype.—Univ. of Calif. at Los Angeles, Invert. Paleo. Cat. nos. 21851 and 28997.

Type locality.—Sitka, Alaska; Recent.

Distribution.—Recent: San Diego to Sitka Alaska. Living in waters ranging from approximately 2 to 19 degrees Centigrade and at depths of approximately 30 fathoms or less.

Remarks.—The varices of the Alaskan forms are usually larger and more curved than those farther south.

CERATOSTOMA BURNETTI (Adams & Reeve), 1850)
Pl. 3, figs. 2,4,6

Murex burnetti Adams & Reeve, 1850, p. 38, pl. 8, figs. 4a,4b.
Murex coreanicus Adams, 1853, p. 72.

Hypotype.—Stanford Univ. Paleo. Type Coll. no. 8495.

Type locality.—Japanese waters 3–27°C.; Recent.

Remarks.—Similar to *C. foliata* but sculpture between varices not as strong, older whorls more rounded, and tooth slightly larger.

CERATOSTOMA DELORAE Hall, 1958
Pl. 3, figs. 8–10

Ceratostoma delorae Hall, 1958.

Description.—Shell heavy, with three whorls and three prominent thick varices continuous from body whorl to spire; aperture ovate; spire low, with indistinct suture; spiral sculpture consisting of 7 distinct and 2 indistinct slightly nodose ribs on the body whorl, with 2 ribs on the penultimate whorl; axial sculpture faint.

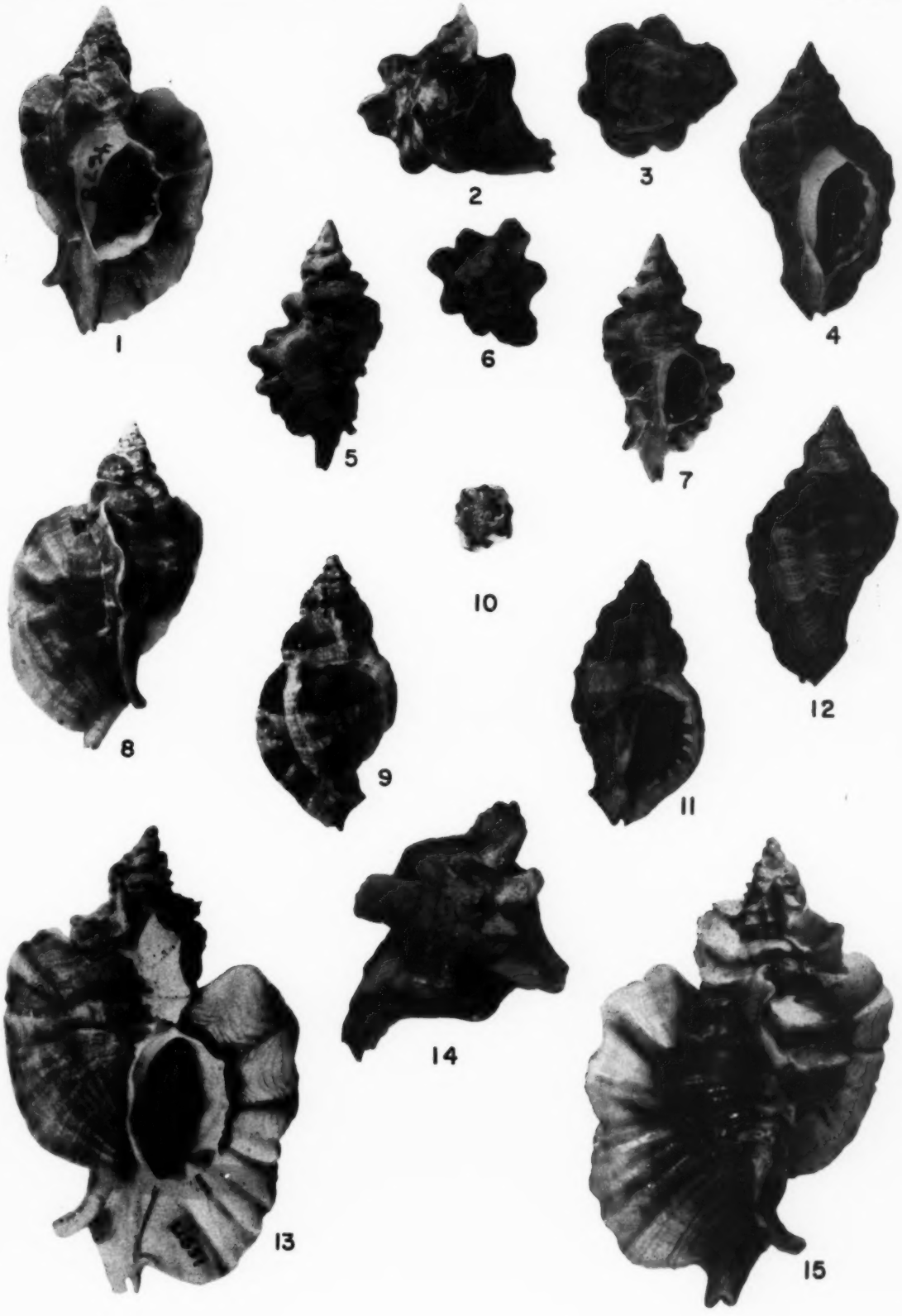
Dimensions.—Height, 62 mm.; width, 38 mm.

Holotype.—Stanford University Type Coll. no. 8473.

Occurrence.—L.S.J.U. loc. 3245. Oursan sandstone, Middle Miocene.

EXPLANATION OF PLATE 61
All figures ×1, except Fig. 10, which is ×½

FIGS. *1,2,8—Ceratostoma nuttalli* (Conrad). UCLA Hypotype Cat. no. 28995. Southern California, Recent.
3,4,12—Ceratostoma nuttalli (Conrad). UCLA Hypotype Cat. no. 28994. Southern California, Recent.
5–7—Ceratostoma fournieri (Crosse). Stanford Univ. Paleo. Type Coll. Hypotype no. 4893. Japan, Recent.
9–11—Ceratostoma rorifluum (Adams and Reeve). Stanford Univ. Paleo. Type Coll. Hypotype no. 8494. Japan, Recent.
13–15—Ceratostoma foliatum (Gmelin). UCLA Hypotype Cat. no. 21851. Howkan, Alaska: Recent.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Remarks.—The age range of *Ceratostoma* has previously been from Upper Miocene (?) or Pliocene to Recent. This species is from Middle Miocene rocks and thus constitutes an extension of the time range for the genus. Since the present day forms that most closely resemble *C. delorae* range northward to Alaska, the implication is that these forms have adapted to relatively cool water through geologic time.

CERATOSTOMA NANNA (Nomland, 1917)

Purpura nanna Nomland, 1917, p. 310, pl. 19, figs. 1a,b; Grant & Gale, 1931, p. 706.

Type locality.—North of Coalinga, California, Miocene.

Type specimen. No. 11315, Univ. Calif. at Berkeley type collection. Upper Miocene, Santa Margarita formation

Remarks.—"This species resembles somewhat closely *Purpura foliata* Martyn: but has a more elongated form, stronger nodes between the varices, a development of fine threadlets between the spiral cords, and the varix on the front side of body whorl projects forward, thus not having the flattened appearance evident on a front view of *Purpura foliata Martyn.*" (Nomland, 1917 p. 310)

CERATOSTOMA PERANGULATUM (Nomland, 1916)

Murex perangulatus Nomland, 1916, p. 206, pl. 11, figs. 1a,b.

Type locality.—Univ. Calif. at Berkeley, locality 2649, west of Coalinga, Calif.; Pliocene.

Type specimen.—In the University of California at Berkeley collection. Etchegoin-Jacalitos formations, Pliocene.

Remarks.—Resembles *C. foliatum*, but is lower spired and has an open canal.

CERATOSTOMA TURRIS (Nomland, 1916)

Purpura turris Nomland, 1916, p. 86, pl. 7, fig. 4.

Type locality.—West of Coalinga at the Univ. of Calif. at Berkeley locality no. 2110, Pliocene.

Type specimen.—At the Univ. of Calif. at Berkeley. From the Etchegoin formation of Pliocene age.

Remarks.—Not as high spired as *C. foliatum*, open canal, ribs on body whorls not as distinct as *C. foliatum.*

CERATOSTOMA PLORATOR (Adams & Reeve, 1850)

Murex plorator, Adams & Reeve, p. 38; Sowerby, p. 25, pl. 10, fig. 89.

Type locality.—Japanese waters 13–27°C., Recent.

CERATOSTOMA ESYCHUS (Dall, 1925)

Murex (Pteropurpura) esychus Dall, 1925, p. 21, pl. 32, fig. 9, pl. 33, fig. 6.

Type locality.—Japanese waters 15–27°C., Recent.

OTHER GENERA

The following genera have at times been confused with the genus *Ceratostoma* and are included to make clear differences.

PTERORHYTIS Conrad, 1868

Pterorytis Conrad, 1862, p. 560; *Pterorhytis* Conrad, 1868, p. 64.

Type.—*Murex umbrifer* Conrad, 1832, by monotypy.

Genus characterized by 4 to 6 varices, foliations on the varices, and a tooth on the anterior portion of the outer lip. Canal completely roofed over.

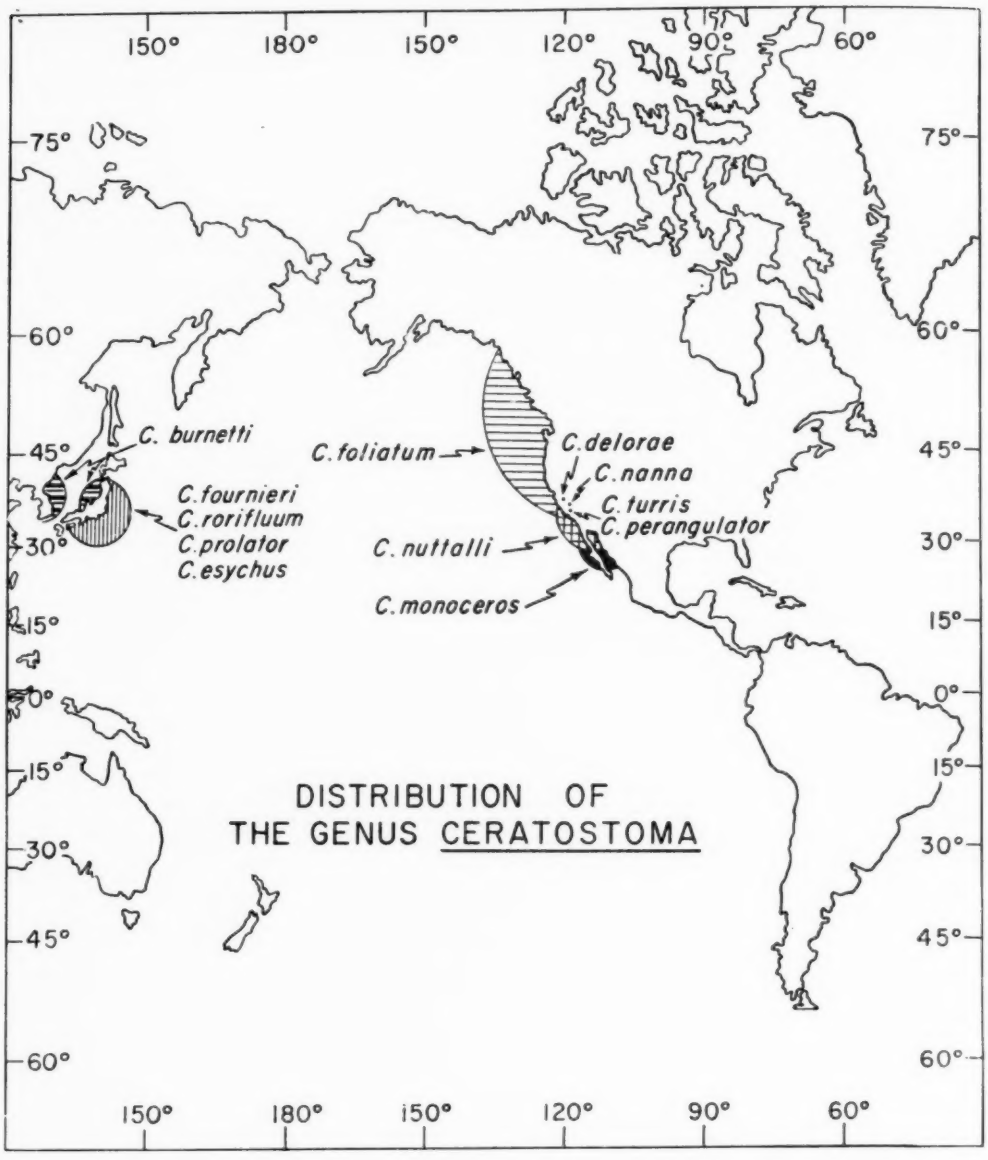
EXPLANATION OF PLATE 62

All figures ×1, except Fig. 7, which is ×½.

FIGS. *1–3—Ocinebrellus aduncus* (Sowerby). UCLA Hypotype Cat. no. 28998. Kii, Japan; Recent. At a depth of 30 fathoms.

4–6—Ceratostoma monoceros (Sowerby). Calif. Acad. Sci. Dept. Paleo. Type Coll. no. 9507. San Ignacio Lagoon, Lower California; Recent.

7–9—Ceratostoma burnetti (Adams & Reeve). Stanford Univ. Paleo. Type Coll. Hypotype no. 8495. Japan, Recent.



TEXT-FIG. 2

PTERORHYTIS UMBRIFER Conrad, 1868
Pl. 3, fig. 6

Pterorhytis umbrifer Conrad, 1868, p. 64.

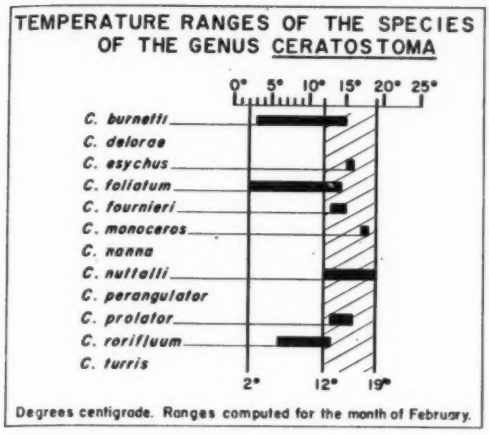
Type locality.—York Town, Virginia
Distribution.—Virginia, Miocene.
Remarks.—4 to 6 varices. Figured by A. Olsson & A. Harbison in Acad. Nat. Sci. Philad. Mono. 8, p. 252, pl. 35, fig. 2.

OCINEBRELLUS Jousseaume, 1880

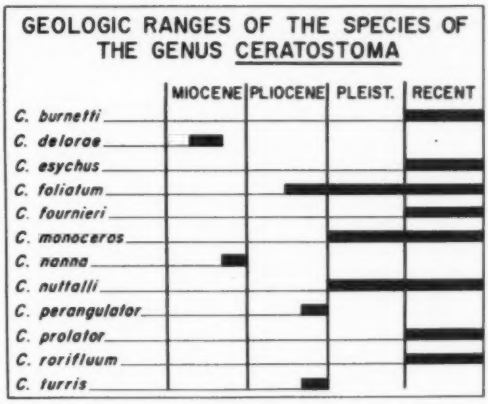
Ocinebrellus, Jousseaume, 1880, p. 355.

Type.—*Murex eurypteron* Reeve, 1845, by original designation. Genus characterized by 4 to 5 varices, and lack of tooth on outer lip, curved varices.

OCINEBRELLUS ADUNCUS (Sowerby, 1834)
Pl. 2, figs. 1–3



TEXT-FIG. *3*



TEXT-FIG. *4*

Murex aduncus Sowerby, 1834, p. 62, fig. 35.
Ceratostoma adunca Sowerby, Hirase, 1954, pl. 109, fig. 11.

Hypotype.—Univ. of Calif. at Los Angeles Invert. Paleo. Cat. No. 28898.

Type locality.—Japan. Recent.

Remarks.—Other *Ocinebrellus* include the species *O. eurypteron* (Reeve, 1845) and *O. falcatus* (Sowerby, 1841).

PTERYNOTUS Swainson, 1837

Pterynotus Swainson, 1833, p. 22, pl. 100.

Genus characterized by three blade-like varices, varices foliated, no tooth on outer lip, weak intervaricial ribbing.

PTERYNOTUS TRIALATUS (Sowerby, 1841)
Pl. 3, figs. 1–3

Murex trialatus Sowerby, 1841, p. 143.

Hypotype.—Univ. of Calif. at Los Angeles, Invert. Paleo. Cat. No. 28999.

Type locality.—Southern California; Pleistocene and Recent. Living in waters from 12 to 24 degrees Centigrade.

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MANUSCRIPT RECEIVED MARCH 1, 1958

EXPLANATION OF PLATE 63

All figures ×1

FIGS. *1–3*—*Pterynotus trialatus* (Sowerby). UCLA Hypotype Cat. no. 28999. San Pedro, California; Recent.

4–7—*Ceratostoma foliata* (Gmelin). UCLA Hypotype Cat. no. 28997. Forrester Is., Alaska; Recent.

6—*Pterorhytis umbrifer* Conrad. Photograph of *P. umbrifer* Conrad in Monograph no. 8, Acad. Nat. Sci. Philad., pl. 35, fig. 2. A. Olsson and A. Harbison. Permission for reproducing figure here kindly granted by A. Olsson. Miocene of Virginia.

8–10—*Ceratostoma delorae* Hall. Stanford Univ. Paleo. Type Coll. Holotype no. 8473. Alameda Co., Calif.; Oursan sandstone, Middle Miocene.

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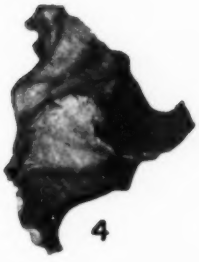

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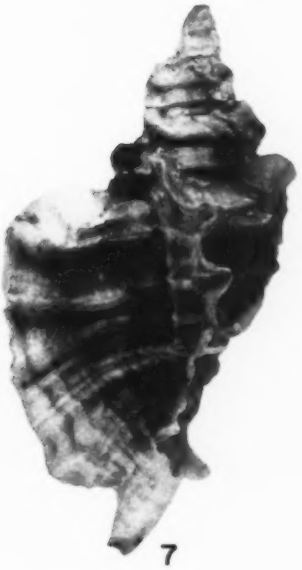

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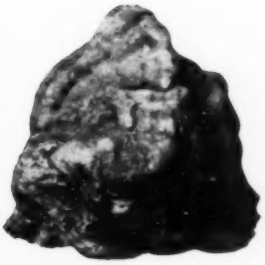

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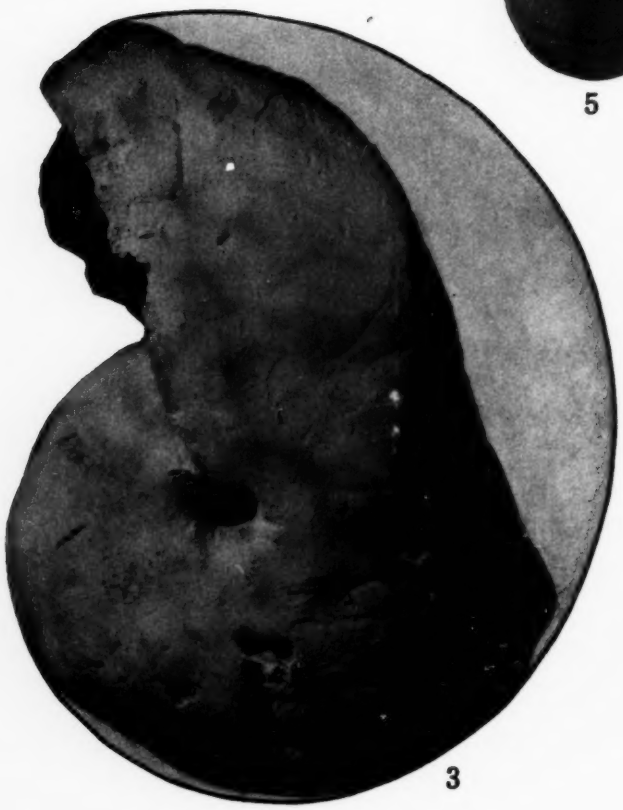

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JOURNAL OF PALEONTOLOGY, V. 33, NO. 3, P. 435–448, PLS. 64–66, 11 TEXT-FIGS., MAY 1959

TERTIARY NAUTILOIDS (*EUTREPHOCERAS* AND *CIMOMIA*) FROM SOUTH AUSTRALIA

B. McGOWRAN
University of Adelaide

ABSTRACT—*Eutrephoceras altifrons* (Chapman and *E. geelongensis* (Foord) from the Lower Miocene of South Australia, intergrade with respect to most characters. They differ, however, in the shape of the umbilical shoulders. The two species, which occur together, are redefined, and Kummel's assignment of them to *Eutrephoceras* is accepted.

The study of new specimens of *Nautilus felix* Chapman from the Upper Eocene of the Adelaide Basin indicates that this species belongs to *Cimomia*. *Cimomia yorkensis* n. sp. is described from beds of the same age.

INTRODUCTION

COLLECTIONS of nautiloids from the Tertiary of South Australia, which have been accumulating for several years in the Department of Geology, University of Adelaide, and in the South Australian Museum, have been studied. Glaessner (1955) described the species of *Aturia*. Species formerly included in *Nautilus* have now been re-examined.

In 1891 Foord described and named *Nautilus geelongensis* from the Tertiary near Geelong, Victoria. Chapman (1915) described *N. altifrons* from the River Murray, South Australia. Kummel (1956) assigned all three to *Eutrephoceras*. "*N.*" *felix* is here assigned to *Cimomia*.

Research on these species and on additional fossils was carried out in 1957 in the Department of Geology at the University of Adelaide. Thanks are due to Dr. M. F. Glaessner for his supervision and assistance. Initial work on the collections was done in 1956 by him and by Mr. D. J. Taylor, who was Research Assistant at the time. Discussion with Miss M. J. Wade (University of Adelaide) facilitated all stages of the work. Dr. B. Daily (South Australian Museum) arranged the loan of material; Dr. B. F. Glenister supplied details of his method of sutural representation and read part of the final manuscript; and Mr. E. D. Gill (National Museum of Victoria, Melbourne) provided a cast of the holotype of *E. altifrons*, and a photograph of the holotype of *C. felix*. A specimen of *C. felix* was loaned by Dr. N. H. Ludbrook (South Australian Department of Mines). Miss A. M. C. Swan drew the locality map.

STRATIGRAPHY

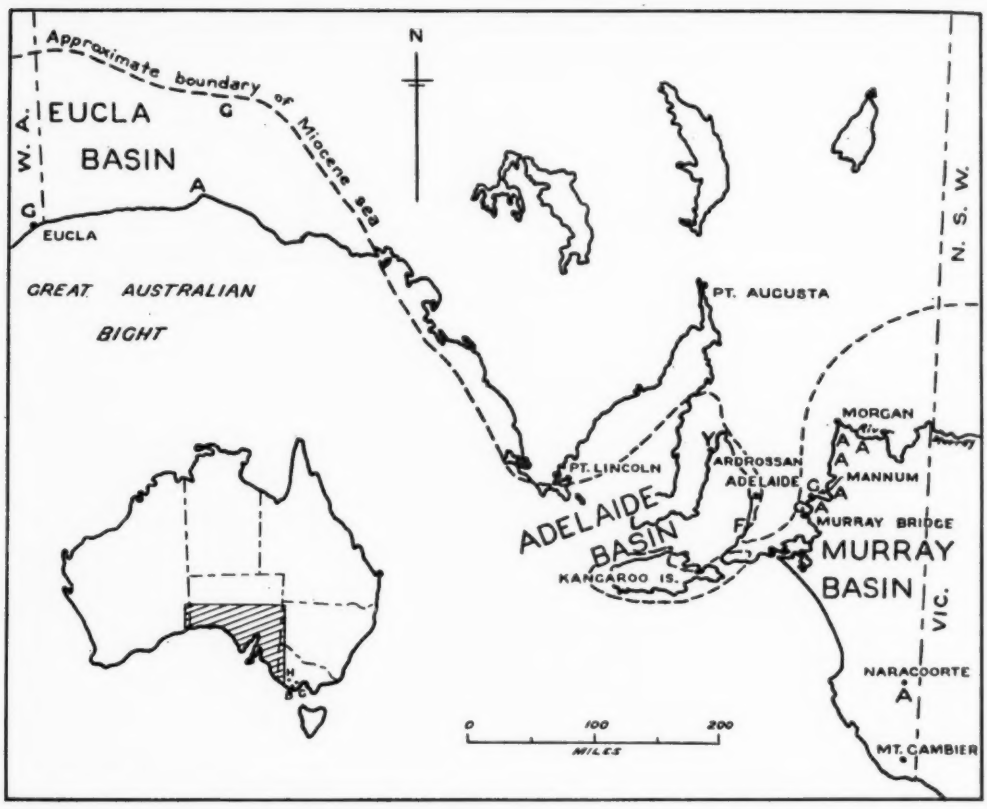
The Tertiary Eucla, Adelaide and Murray Basins opened towards the Southern Ocean. The Eocene species *Cimomia felix* (Chapman) and *C. yorkensis* sp. nov. are known only from the Adelaide Basin; the species of *Eutrephoceras* are found in the Miocene beds of the others.

The Upper Eocene sequence to the south of Adelaide includes the Tortachilla Lime-

EXPLANATION OF PLATE 64

FIGS. *1,2*—*Eutrephoceras geelongensis* (Foord). *1*, from the Lower Miocene Morgan Limestone of Western Flat, River Murray, South Australia, AUGD F15559, ×⅔. *2*, from the Nullarbor Limestone (Lower Miocene), Nullarbor Plains, South Aust., SAM P5958, ×⅔.

3–5—*Eutrephoceras altifrons* (Chapman). *3,4*, Cast of holotype from the Morgan Limestone, probably near Blanchetown, South Australia, Nat. Mus. of Victoria, Melbourne, P4625, ×½. *5*, from the Morgan Limestone, Morgan, South Australia, SAM P6116, ×½.



TEXT-FIG. *1*—Sketch-map showing known occurrence in South Australia of *E. altifrons* (A), *E. geelongensis* (G), *C. felix* (F) and *C. yorkensis* (Y). The occurrence of *E. geelongensis* at Geelong (G) and at Hamilton (H); and of *C. felix* at Brown's Creek (B) is shown on the inset map, in Victoria.

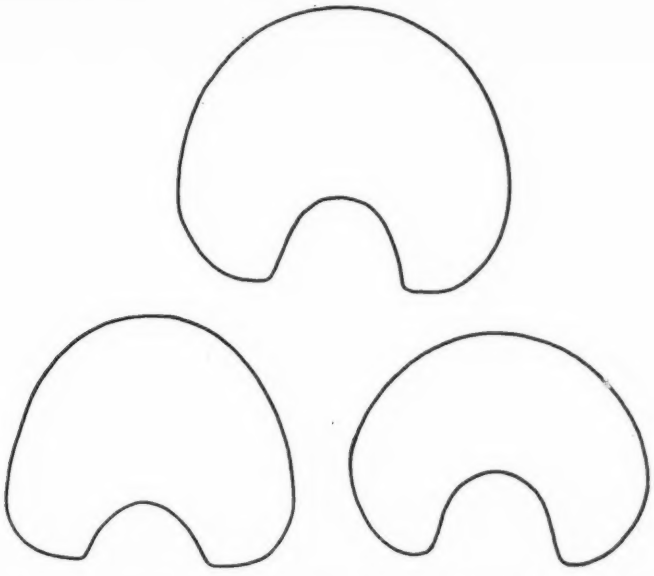
stone and the Blanche Point Marls, from both of which several specimens of *C. felix* have been taken. These formations outcrop on the coast of St. Vincent Gulf. *Hantkenina alabamensis* Cushman, found at the base of the Marls, is the main stratigraphic marker (Glaessner 1951). The uppermost part of the Blanche Point Marls may be of lower Oligocene age; however all definitely identifiable specimens of *C. felix* are from the Upper Eocene. The holotype and other specimens were taken from the Upper Eocene, 7 miles along the strike to the northeast of the coastal exposures.

Eutrephoceras has been found in three units of the mid-Tertiary strata of the Murray Basin (Ludbrook 1957). The highly fossiliferous Naracoorte Limestone of Upper Oligocene to Lower Miocene age contains *E. altifrons*. The Lower Miocene formations exposed along the River Murray carry both species. They are the Mannum Formation, a richly fossiliferous sandy limestone and calcareous sandstone, and the younger Morgan Limestone, a "bryozoal, fine and generally evengrained sandy limestone, frequently gypseous and sometimes marly" (Ludbrook 1957, p. 178).

The Nullarbor Limestone (O. P. Singleton 1954, p. 63) of the Eucla Basin, a hard crystalline limestone, contains both species of *Eutrephoceras*. According to Singleton the abundant molluscs suggest correlation with the Lower Miocene Batesfordian Stage of Victoria.

SYSTEMATIC DESCRIPTIONS

Family NAUTILIDAE d'Orbigny, 1840
Subfamily NAUTILINAE d'Orbigny, 1840
Genus EUTREPHOCERAS Hyatt, 1894



TEXT-FIG. 2—Cross-Sections of *Eutrephoceras geelongensis* (Foord), based on internal moulds. Spec. F15560 (top), P5958 (lower left) and F15559. ×⅔.

Type species: Nautilus Dekayi Morton, 1834.

EUTREPHOCERAS GEELONGENSIS (Foord)
Pl. 64, figs. 1,2; pl. 66, figs. 3,4;
text-figs. 2–5, 9.

Nautilus geelongensis FOORD, 1891, p. 332, fig. 69.
CHAPMAN, 1915, p. 354–356, pl. 4, figs. 7–9.
Eutrephoceras geelongensis KUMMEL, 1956, p. 335.

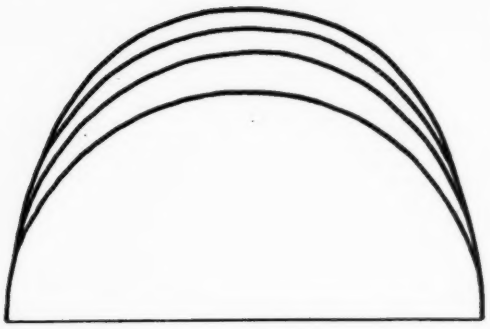
The description of the holotype by Foord is brief but accompanied by a clear and detailed woodcut. Chapman elaborated on Foord's description, mainly with regard to characters of the shell and to geographic distribution of the species.

Description.—The maximum diameter of one of the largest specimens is more than 210 mm. The conchs are subglobular in shape, and the whorls are well rounded ventrally, with slight lateral compression. The depth of the dorsally impressed zone is slightly less than one-third the height of the camera, and the height is less than the width. Some of the specimens have living chambers more prominently flayed out orad than do the others in which the living chambers are preserved.

Variation in the ventral and lateral regions is shown in fig. 2. These cameral cross-sections are planes through the points on the dorsum and venter which are midway between the two sutures.

In order to study this variation more easily, the following procedure was carried out. The height/width ratio was determined, using the maximum width, and the height from its level to the ventral midline. This was done for each specimen, using camerae from as nearly equivalent stages of development as possible. Hence the height of each specimen could be recalculated for constant width, and the intraspecific variation of cross-sectional area with height found. Fig. 3 shows that this variation is probably continuous. Height must be squared for valid comparison with area (Simpson 1957, p. 60). The correlation coefficient of 100 $(\text{height})^2$ with area is 0.99.

In most specimens the umbilicus is over 20 mm. in diameter, although this was measured on internal moulds only. Material from the Lower Miocene of western Victoria includes the original, unaltered shell from the umbilical region of an adult individual. In this it is thickened, and definitely imperforate. A small amount of matrix in specimen SAM P5932 is an external mould of the umbilicus, which was therefore narrowly



TEXT-FIG. 3—Variation in *E. geelongensis*. Cross-sections adjusted to constant diameter.

perforate. The whorl is of a pre-adult stage, however, and fairly tightly coiled. The outer umbilical shoulder is in all cases well rounded, contrasting with the much more prominent inner shoulder.

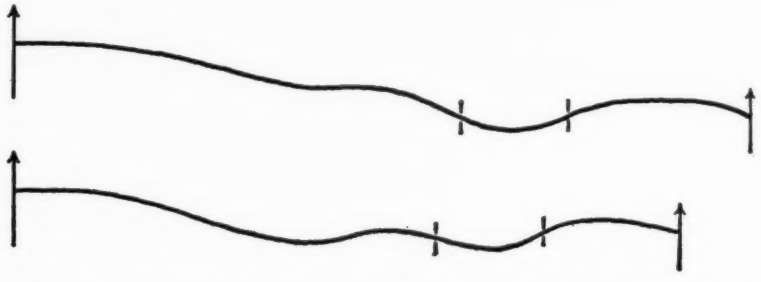
The siphuncle (orthochoanitic) consistently is situated about midway between the dorsum and the venter.

There are about 12 camerae in the outer volution, apparently regardless of the stage reached in growth. The distance between successive septa tends to increase during growth. This increase is not constant, as occasional camerae are shorter than are the adjacent ones. The living chamber occupies about one-half the last whorl.

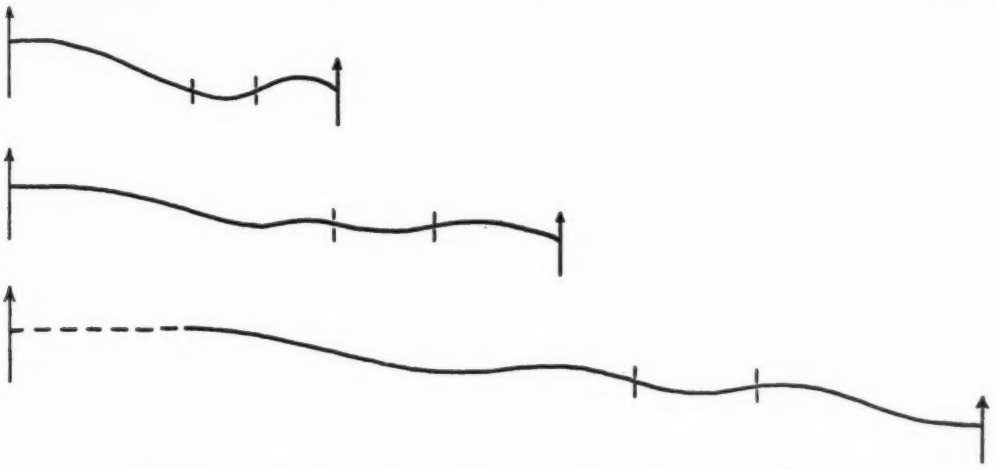
Apart from sutures, the only intrinsic markings on the internal moulds are a slightly raised ridge on the ventral midline of one specimen, and, flanking this ridge on either side, a narrow, barely discernible furrow. These markings become more pronounced with growth, and are not visible in the earlier part of the outer whorl. The feature does not appear to be common in this genus or in *Cimomia*, and is not so prominent as the markings described on the venter of *C. pusilla* (Haas and Miller, 1952, p. 334, pl. 21, fig. 3).

Dr. B. F. Glenister has kindly supplied details of his method of sutural representation. As he has pointed out, the drawing of the relatively simple nautiloid sutures presents different technical problems from that of the ammonoids. His method is here quoted: " . . . The specimens are generally too bulky for convenient camera lucida treatment. For these large specimens I establish a 'centre line.' This is an actual pencil line on the specimen. It represents the line along which the plane which contains the axis of the umbilicus and passes approximately through the mid-height of a septum, meets the inside of the shell. In practice the 'centre line' is drawn from the centre of the umbilicus through the suture so that the crests and troughs of successive saddles and lobes are approximately equally distant from the line. The tangent at the point where the line crosses the venter should be at right angles to the centre line. Once this straight centre line is established then it should be subdivided into a number of convenient lengths. These lengths are then duplicated at a suitable scale on drawing paper. Sutural elements can then be drawn in with respect to the centre line and its subdivisions."

The sutures (fig. 4) have a broad, almost flat ventral saddle, a shallow but clearly defined lateral lobe, and a shallow lateral saddle on, or just ventrad of, the umbilical shoulder. This is referred to as the ventrolateral saddle. Another rather shallow lobe (on the umbilical wall) and the saddle follow, and pass into a broad dorsal lobe. In



TEXT-FIG. 4—Sutures of *E. geelongensis*. Spec. F15560 (top) and F15559. ×$\frac{3}{4}$.



TEXT-FIG. 5—Development of suture in *E. geelongensis* (spec. F15561). ×¾.

the centre of the latter, an annular lobe is prominent in the younger stages of growth.

Three sutures from the one specimen, in their order of maturity, have been figured (fig. 5). These show ontogenetic changes, with the formation of the ventrolateral saddle as the main development in sutural form. The figured series shows the origin of this saddle during adolescence, on the ventrolateral flank of the original lateral lobe.

Prominence of the sutural features in different specimens varies considerably, but appears to be largely a function of the stage reached in growth. Thus in the larger specimens the sutures are straighter, as their length increases both absolutely and relative to the amplitude of the lobes and saddles.

Age.—Lower Miocene.

Material.—University of Adelaide (AUGD) F15559–F15561. South Australian Museum (SAM) P858, P5615, P5931–P5933, P12435.

Occurrence.—Five specimens of *E. geelongensis* are available from the Nullarbor Limestone. One is from near Eucla, and one from near Watson; the precise localities of the others are unknown.

The matrix of three unlabelled individuals indicates that they were collected from the Mannum Formation in the Murray Basin. Recorded localities of occurrence in the Morgan Limestone are Overland Corner and "Murray View," nine miles from Waikerie.

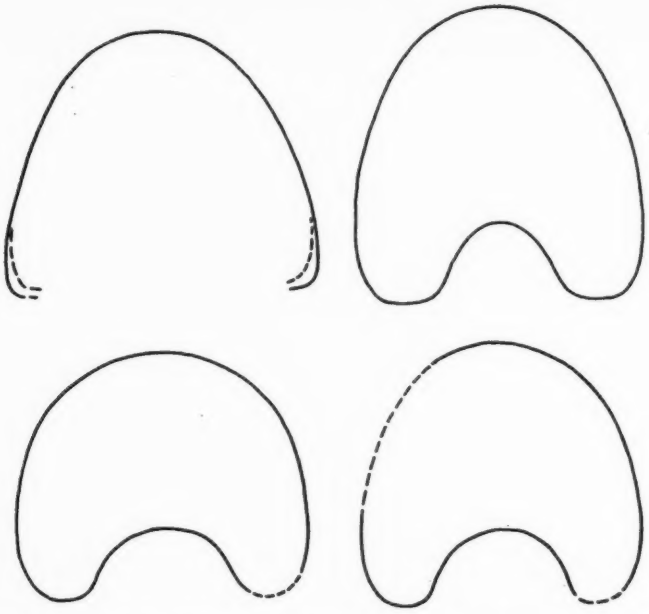
The holotype was collected near Geelong, Victoria. A specimen in the Adelaide University collection came from the Muddy Creek Marls near Hamilton, Victoria (Lower or Middle Miocene, Gill 1957). Chapman records the discovery of a specimen of *E. geelongensis* in the Lower Pliocene of the Grange Burn, to which Muddy Creek is a tributary. The Lower Pliocene here (separated from the Middle Miocene by a disconformity) contains a cast of *Aturia australis* McCoy, derived from the Miocene, and Chapman's specimen of *E. geelongensis* is probably also reworked.

EUTREPHOCERAS ALTIFRONS (Chapman)
Pl. 64, figs. 3–5; pl. 65, fig. 8; pl. 66, figs. 1,2; text-figs. 6–9

Nautilus altifrons CHAPMAN, 1915, p. 356–357, pl. 5, figs. 10–12, pl. 6, fig. 13.
Eutrephoceras altifrons KUMMEL, 1956, p. 332.

Chapman distinguished this species from *E. geelongensis* by the compressed form of the shell and its consequently high apertural front. He mentions also more undulate sutures, the open and deep umbilicus, the almost quadrate aperture and the ventral siphuncle. Much of the South Australian material is considered to belong in this species, but it is proposed that the original specific diagnosis should be revised.

Description.—The specific name implies a



TEXT-FIG. 6—Cross-Sections of *E. altifrons* (Chapman). The holotype (upper left) shows the thickening of the shell on the shoulders; the others (spec. F15565, F15564, P5960) are based on internal moulds. $\times\frac{3}{5}$.

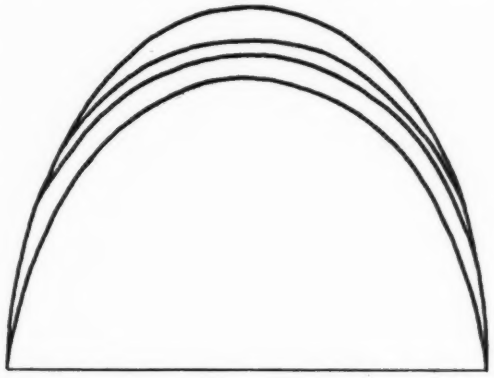
high apertural front. Thus the aperture of the holotype was stated to be 124 mm. high and 103 mm. wide (Chapman p. 356). This height/width ratio is somewhat high, as the aperture as preserved in the holotype is not a true cross-section of the outer whorl.

All specimens have arched whorls, flattened laterally and gently rounded ventrally (fig. 6). The depth of the dorsally impressed zone is about one-third the camera height. Some specimens have living chambers distinctly flayed out orad; others do not.

The specimens were studied in the same way as those of *E. geelongensis* and, as in the latter, a probably continuous series was found (fig. 7). The coefficient of correlation of 100 (height)^2 with the area is 0.99.

The position of the orthochoanitic siphuncle varies considerably. Determination of position involved the measurement of the perpendicular distance from the siphuncle to the dorsum and to the venter, and hence separate camerae in a sufficiently good state of preservation were needed. It was noted that observation without measurement was often unreliable. In some individuals the siphuncle is central or slightly dorsal; in others it is decidedly ventral. No relationship between the position of the siphuncle and the height of the camera was found with the material available.

The umbilicus has a maximum diameter of 25 mm. where the major diameter of the whorl is 160 mm. Neither of the umbilical



TEXT-FIG. 7—Variation in *E. altifrons*, with sections adjusted to constant diameter.

shoulders is well rounded, although the outer one is sometimes more so. The resultant squaring of the umbilical region gives the umbilicus a stepped appearance both on the internal moulds and to a lesser extent on the replaced shell of the holotype, as noted by Chapman (1915, p. 356). Two specimens have the shells replaced by selenite; these are thicker in the umbilical region than on the ventral and lateral parts of the conch. The umbilicus, however, is open and deep, with matrix plugs forming external umbilical moulds in specimens without shell.

Many specimens of *E. altifrons* have a distinctive suture (text-fig. 8). The ventral saddle is flat or slightly retuse, and flanked by a very broad lateral lobe, and a small saddle either on the umbilical wall or slightly to one side of it. In the more mature parts of the phragmocone the dorsal lobe is broad and shallow and the annular lobe, present in some sutures, tends to become reduced.

Remarks.—Variation in the relative prominence of the different sutural features is quite pronounced (text-fig. 8). Some sutures are almost straight.

Ontogenetic change in the sutural form, where noticeable, consists of general decrease in relative depth of the lateral and dorsal lobes, and reduction of the annular lobe, with increasing maturity.

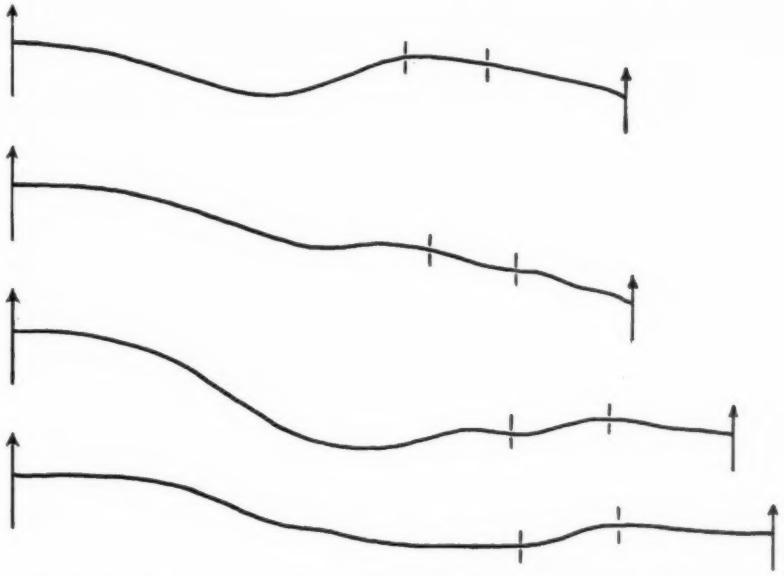
The height/width ratios of the camerae were found to vary slightly within the one individual. No trend was noticed, as the ratio increased, decreased, or oscillated in different specimens. It is therefore tentatively suggested that this indicates a response of each individual to varying environmental conditions encountered during ontogeny. A firmer decision could be made on this matter if more were known about such responses in living *Nautilus*, and about the rate of formation of septa.

Age.—Upper Oligocene–Lower Miocene.

Material.—University of Adelaide F15562–F15569. South Australian Museum P5231, P5933, P5955, P5959, P5960, P6116, P9099, P10907, P12434, P12435.

A cast of the holotype, which is in the National Museum in Melbourne was kindly made available by Mr. E. D. Gill. Several less well preserved specimens in the University collection have not been catalogued.

Occurrence.—The only available specimen from the Eucla Basin was found in the White Well Cave, two miles northwest of the White Well Homestead, in the Nullarbor Limestone.



TEXT-FIG. 8—Sutures of *E. altifrons*. Spec. F15565 (top), F15562, F15569, F15563. ×¾.

The collections studied include six specimens from the Naracoorte Limestone of James' Quarry, ½ mile from Naracoorte. This is the oldest known occurrence of *E. altifrons* (Uppermost Oligocene to Lower Miocene).

Several specimens were found at Mannum. Others labelled "Murray Cliffs" are contained in matrix characteristic of the Mannum Formation.

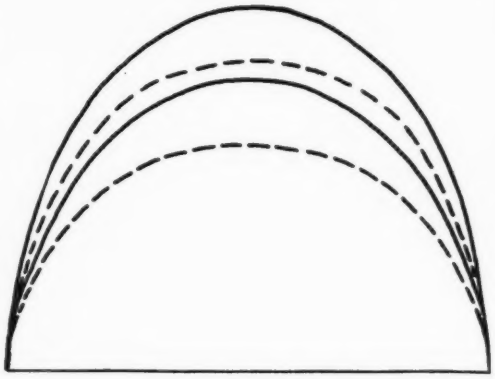
The remainder were collected from the Morgan Limestone on the River Murray. Most are from the cliffs bordering the river, and recorded localities include Blanchetown, Wood's Flat and Waikerie. The species is also known from the building stone quarry at Overland Corner.

COMPARISON OF E. ALTIFRONS AND E. GEELONGENSIS

Two features of the material described above are the variation within each species and the overlap of this variation. Hence the need to evaluate the relative taxonomic importance of as many characters as possible.

Overlap in the ventral and lateral cross-sectional outline of the conch is shown in text-fig. 9. This outline is therefore not completely diagnostic in itself, although *E. geelongensis* tends to be more inflated. Tests for the regression of (cross-sectional area) on (height^2×100) for each species showed no significant difference. Since the correlation of these variables is almost perfect in each case, it seems that the other factors controlling the degree of inflation or compression are either constant or insignificant.

The umbilical shoulder is of two types, this character being the only one not showing pronounced variation or overlap. The umbilicus itself varies in width but is narrower or completely infilled in *E. geelongensis*, and the whorls are more constricted in this species.



TEXT-FIG. 9—Comparison of *E. altifrons* and *E. geelongensis* (dashed).

A few individuals of *E. altifrons* have sutures very like those of *E. geelongensis* (compare text-fig. 4, spec. AUGD F15560, and text-fig. 8, spec. AUGD F15563). In the majority the ventrolateral saddle is absent or poorly developed.

The only feature completely reliable for distinguishing the species seems to be the form of the umbilical shoulders. As a rule the form of the suture is considered to be the character most important in the taxonomy of Tertiary nautiloids. This is due largely to the claim that sexual dimorphism and other intraspecific variations cause important differences in both the general inflation of the conch and the umbilical region of modern *Nautilus* (Miller 1947, p. 16–17, 24).

Although the characters other than the umbilical shoulders show considerable variation and partial overlap, their differences are sufficiently correlated with the shoulder types to provide the necessary complex for taxonomic discrimination. Other features often used for specific distinction within *Eutrephoceras*, but of little use here, include the presence or absence of an annular lobe, and the position of the siphuncle. The latter

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EXPLANATION OF PLATE 65

FIGS. *1–7*—*Cimomia felix* (Chapman). *1,2* (AUGD F15551) from the Upper Eocene Tortachilla Limestone, Christies Beach, South Australia; *1*, ×¾, *2,3,4*, ×⅔. *5,6*, from the Upper Eocene of Happy Valley, South Australia, SAM P5956, ×¾. *7*, holotype (Nat. Mus. Victoria) from Happy Valley, ×1.

8—*Eutrephoceras altifrons* (Chapman). Specimen SAM P6116 from the Morgan Limestone, Morgan, South Aust., ×⅔.

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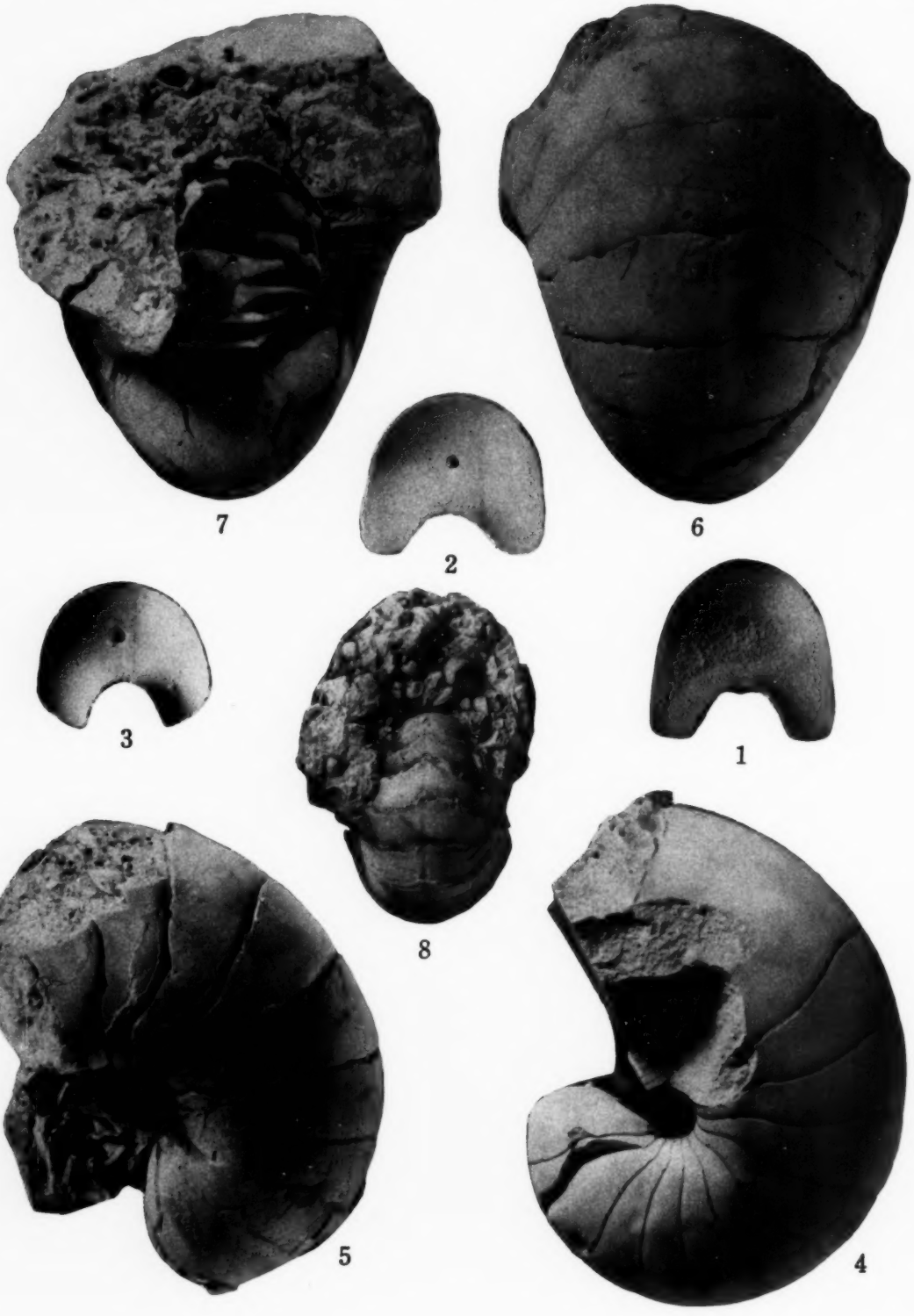
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varies much more in *E. altifrons* than in *E. geelongensis*, and tends to overlap.

The differences in hard-part morphology between *E. altifrons* and *E. geelongensis* are more complex than those usually attributed to sex-linked variation in this group. More likely, in this connection, is the possibility that the oral flaying out of the living chamber, noticed in certain individuals of both species, has a sexual correlation.

Other possible explanations for the overlap in variation include the existence of geographic or ecologic subspecies, or of intrapopulational polymorphic variants. The first two possibilities are not supported by the horizons or localities of occurrences, even allowing for the often extensive post mortem drift to be expected of nautiloid conchs before they sink on becoming waterlogged, subsequently being embedded and preserved. This factor would also destroy any evidence of ecological incompatibility. The third view is hardly tenable, as several characters, correlated to a greater or lesser degree, are involved in the variation.

The genetic position of *E. altifrons* and *E. geelongensis* is indicated only by degree of sutural sinuousity, and is not clearcut. Certain individuals, especially of *E. altifrons* have sutures almost as sinuous as those of several species placed in *Cimomia*. Since the lobes and saddles tend to become less pronounced with maturity, and some sutures are almost straight, the two species are placed in *Eutrephoceras*, with the reservation that they tend toward *Cimomia*. It is generally accepted that *Cimomia* evolved from Eutrephoceratid stock, either during the Upper Jurassic only, or at different times thereafter as well. The presence of morphologically intermediate species on several stratigraphic levels could indicate a polyphyletic origin for *Cimomia*, or parallel evolutionary patterns for *Cimomia* and *Eutrephoceras*, or both. The first possibility is very likely but parallel evolution has probably occurred also. Comparison of the diagnoses for the two genera (Miller 1947, p. 27, 41) shows that the distinguishing features (of varying value) are the form of the suture, inflation of the conch and presence (in *Cimomia*) of growth lines. Observed variation in *E. altifrons* and *E. geelongensis* indicates that a monophyletic origin for *Cimomia* is most unlikely; several lineages probably crossed the ill-defined line separating the two genera.

Subfamily HERCOGLOSSINAE Spath 1927
Genus CIMOMIA Conrad 1866

Type species: Nautilus Burtini Galeotti, 1837.

CIMOMIA FELIX (Chapman)
Pl. 65, figs. 1–7; text-fig. 10

Nautilus felix CHAPMAN, 1915, p. 357, pl. 6, fig. 14, pl. 7, fig. 15.
Eutrephoceras felix KUMMEL, 1956, p. 335.

The holotype of this species is in the Dennant Collection in the National Museum, Melbourne. Chapman's type description is rather inadequate, as he was apparently unable to examine the immature volutions.

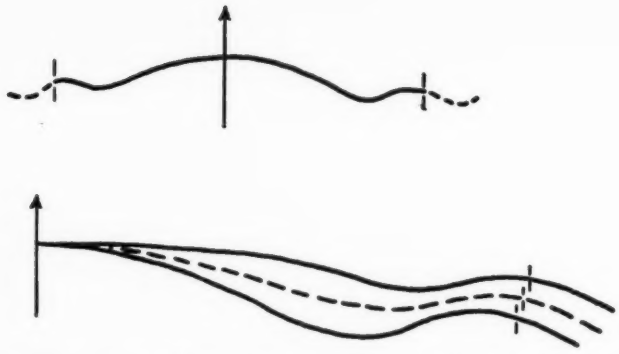
Description.—The maximum diameter of the largest undistorted specimen is slightly less than 150 mm. The largest individual is slightly flattened, and over 215 mm. in diameter. In *C. felix* all the whorls are arched, well rounded ventrally, and laterally flattened. The width of the mature camerae is about the same as the height, and the depth of the dorsally impressed zone, about one-third the latter.

EXPLANATION OF PLATE 66

FIGS. *1,2*—*Eutrephoceras altifrons* (Chapman). *1*, from the Nullarbor Limestone, White Well Cave, South Australia, SAM P12374, ×½. *2*, locality unknown but probably from the Morgan Limestone, River Murray, South Aust., SAM P5931, ×½.

3,4—*Eutrephoceras geelongensis* (Foord). *3*, from the Morgan Limestone, Western Flat, South Aust., AUGD F15559, ×½. *4*, from the Nullarbor Limestone, SAM P5950, ×⅔.

5–8—*Cimomia yorkensis* n. sp. *5–7*, holotype from the east coast of Spencer Gulf, probably Eocene near Ardrossan, South Australia, AUGD F15558, ×⅔. *8*, paratype, probably from the same locality, AUGD F15558, ×¾.



TEXT-FIG. *10*—Sutures of *Cimomia felix* (Chapman), from an adolescent whorl (spec. F15551) and from a mature specimen (spec. F15550). ×1.

There is some variation in the degree of compression of the immature conch, as shown by the comparison of two undistorted specimens (pl. 2, figs. 2, 3). The uncrushed adult forms are similar in outline to the young laterally compressed individuals.

The body chamber occupies about half the last volution, which also has 8–10 camerae. The adoral edge of the area of muscle attachment is very distinct on the body chamber of one specimen. It is sinuous, and almost identical in shape and position with that found in *Nautilus pompilius* (Miller 1947, pl. 4).

A few juvenile individuals, on which no shell is preserved, have a plug of external mould in the umbilicus, indicating that the later was perforate. Those adult forms with much of the shell remaining, however, have the umbilicus filled with callus. This situation could be analogous to that found in *Nautilus pompilius* Linné, where different varieties have either perforate or imperforate umbilici (Miller 1947, p. 16–17). It may, on the other hand, indicate a characteristic ontogenetic development, in which the umbilicus becomes filled in the adult stage. The umbilical shoulders are not particularly well rounded, although the outer one is slightly more so than the inner.

The siphuncle is orthochoanitic, and centro-ventral in position (thus on a camera 35 mm. in height, the 2 mm. wide siphuncle is 12 mm. from the dorsum and 8 mm. from the venter).

The surfaces of the internal moulds are generally smooth, and devoid of any significant markings other than sutures. Prominent growth lines are seen on those specimens retaining part of the original shell, and they have shallow but distinct lateral sinuses. Whether they also have a ventral sinus could not be determined due to preservation. A young individual with a well preserved shell also bears fine longitudinal striations. These are absent from the more mature specimens, a situation also found in *N. pompilius* (Miller 1947, p. 16).

The sutures have a broad ventral saddle flanked by a lateral lobe, and a rather narrow saddle slightly ventral to the umbilical shoulder. These features are prominent in both young and mature specimens (fig. 10). A rather shallow dorsal lobe could be seen in a few specimens. Some show annular lobes in the younger parts of the phragmocones.

Remarks.—The suture of *Cimomia* has, typically, "a broad very shallow broadly rounded or slightly retuse ventral saddle, a broad shallow broadly rounded lateral lobe, a narrower higher rounded lateral saddle (located near the umbilical shoulders), a broad rounded lobe on the umbilical wall, and a fairly prominent internal lateral saddle that extends to a broad rounded dorsal lobe" (Miller 1947, p. 39, 41). This applies to *C. felix* (at least ventrad of the inner umbilical shoulders), whose adult suture is similar to that of *C. pseudobouchardianum* (Spengler 1910) as figured by Kummel (1956, p. 448). The latter suture is not complete. *C. blakei* (Avnimelech) resembles *C. felix* in the form of the suture in the ventrolateral region. The affinities of *felix* with *Cimomia* are therefore greater than with *Eutrepho-*

ceras, especially with regard to the well developed lateral saddles. The two lobes on the suture, flanking the lateral saddle, are about the same size, or much more nearly so than is the case in *Nautilus*, and it is considered that *C. felix* does not belong to this genus. The holotype, which is refigured here (pl. 2, fig. 7), is considerably worn in the lateral areas, so that the sutures appear less sinuous than they are. This is apparently the reason for the assignation of *C. felix* to *Eutrephoceras* by Kummel (1956, p. 335).

The annular lobe, found in all South Australian species, is of little taxonomic importance. It is sufficient to mention that although Miller (1947, p. 26) states that *Cimomia* does not have this lobe, Kummel (1956, p. 333) has placed "*Nautilus*" *blakei* in *Cimomia*, on the basis of its suture, and *C. blakei* has an annular lobe. The tendency of this lobe to degenerate in the more mature parts of nautiloid phragmocones, further limits its use.

A juvenile specimen of the Miocene "*Nautilus*" *balcombensis* Chapman (reclassified by Kummel under *Eutrephoceras*) has been examined. Its sutures are similar to those of *C. felix*, but a little less sinuous. The longitudinal striations which characterize the young stages of *E. balcombensis* are much more prominent than in *C. felix*.

Glenister, Miller and Furnish (1956) have recently described a new species, *Cimomia tenuicosta*, from the late Campanian—early Maestrichtian of Western Australia. Although the sutures of the young individual figured (said to be atypical: p. 496) are very similar to those of *C. felix* in the early stages, the adult sutures of the former species have a decidedly more pronounced lateral saddle.

Age.—Upper Eocene.

Material.—University of Adelaide F15550–F15556.

South Australian Museum P5956.

The University collection also contains several flattened or otherwise poorly preserved specimens which have not been catalogued.

Occurrence.—*C. felix* is commonly found in the coastal exposures of the Tortachilla Limestone and Blanche Point Marls, at Christies Beach, Port Noarlunga and Maslin Bay, south of Adelaide. Several specimens have been taken from the marls at Blanche Point, and one was found in the same formation during the drilling of Scammet's Well, Willunga.

Specimens from Happy Valley (the type locality) were embedded in the clayey, glauconitic marl which is an equivalent of the Tortachilla Limestone of the coastal sections.

The species has been found at Brown's Creek, Victoria, in the Brown's Creek Marls. These beds contain *Hantkenina alabamensis compressa* Parr, and are of Upper Eocene age.

Cimomia Yorkensis, n. sp.
Pl. 66, figs. 5–8; text-fig. 11

This is based on two specimens, which can be distinguished from all previously described Australian species.

Description.—The holotype is a large individual consisting of at least three volutions, with a maximum diameter of about 130 mm. This figure is less than if the living chamber had been preserved. The paratype is smaller and exhibits an adolescent whorl, with the venter of the latter bearing the broken inner edges of the succeeding whorl.

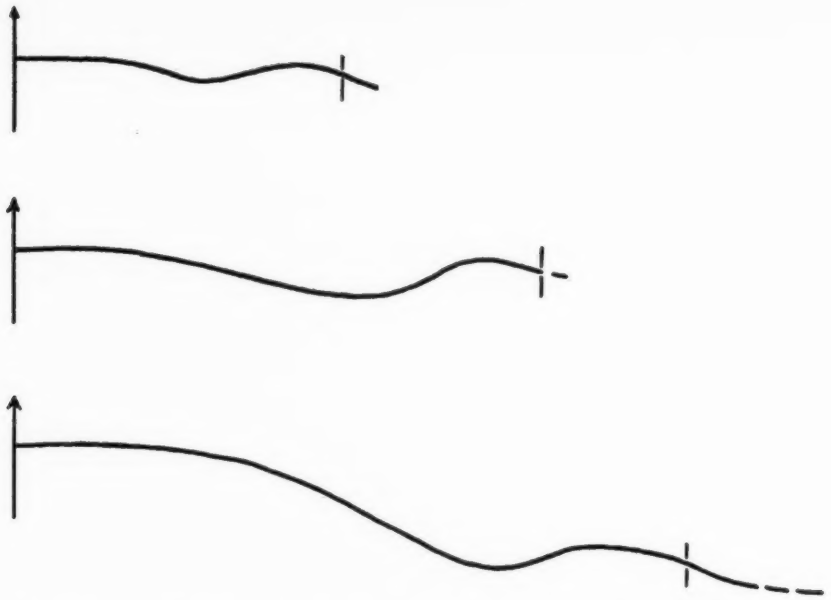
The mature whorl of the holotype has a broad dorsally impressed zone. The last camera before the living chamber is about 70 mm. high and 100 mm. wide. The ninth camera from the body chamber is 38 mm. high, 60 mm. wide (approx.) and the dorsally impressed zone is about 12 mm. deep.

The umbilical walls are steep, and the umbilicus is perforate, with a maximum diameter of about 12 mm. There is a strong thickening of the shell in this region.

The siphuncle is small and orthochoanitic, and centrodorsal in position.

A narrow but distinct ridge occurs on the ventral midline of all camerae of the holotype. It is similar to that found in *E. geelongensis*. The surface of the internal mould is generally smooth, without markings other than sutures. The replaced shell of the holotype shows growth lines which curve posteriorly to form a hyponomic sinus. Lateral sinuses were not definitely seen.

Each suture has a broad, almost flat ventral saddle, flanked by a broad shallow lateral lobe, and a more distinct lateral saddle on, or slightly ventral to, the umbilical



TEXT-FIG. *11*—Sutures of *C. yorkensis* sp. nov. (a) mature suture of the holotype; (b) less mature, but on the same whorl; (c) adolescent suture (paratype). ×1.

shoulder (fig. 11). This is evident in both the adolescent and the more mature sutures. Apart from noting the presence of an annular lobe, the sutures could not be studied beyond the umbilical wall in either specimen.

Remarks.—Although this species does not closely resemble any of those described by Chapman (1915), it is more like *C. felix* than the others. This resemblance is in the form of the suture only; features distinguishing the new species from *C. felix* include the position of the siphuncle (which may be significant), the lower height/width ratio in the mature camerae, the perforate umbilicus in the adult stage, and the steeper umbilical walls. In cross-section the conch of *C. yorkensis* is more triangular than that of *C. felix*, as the outer umbilical shoulder is more angular (at least in the adult) and the lateral areas are flattened. *C. felix*, although not characterized in the adult stage by a highly inflated shell, is more smoothly rounded than is *C. yorkensis*. Thickening of the shell on the shoulders, more pronounced in *C. yorkensis*, may on the evidence of *Nautilus pompilius* Linné (Miller 1947, p. 16–17), be of little significance.

Age.—? Upper Eocene.

Material.—University of Adelaide F15558 (holotype), F15557 (paratype).

Occurrence.—Both specimens of *C. yorkensis* were found on Yorke Peninsula, but the exact location is unknown. The foraminiferal content of the silicified matrix does not indicate the age conclusively. The matrix is very similar to parts of the Blanche Point Marls, and the specimens were probably collected from the Upper Eocene marls near Ardrossan.

PRESERVATION

Almost all the material consists of internal moulds, several of which are exceptionally well preserved.

(a) *Miocene Species.*—All but three individuals of these species are limestone moulds only, the matrix being largely calcarenite of varying degrees of porosity, density and recrystallization, and with differing amounts of marl and inorganic arenaceous material in addition to the dominant organic fragments. These differences in matrix are correlated with the units in which the fossils occur (Ludbrook 1957; see also remarks on stratigraphy in this paper).

Separate camerae are preserved in this way, as are the living chambers of some individuals. The septa and siphuncle are seen in one specimen only of *E. altifrons*, as gypsum casts. The outer shell of the conch is replaced by gypsum in the holotype of *E. altifrons* and in one other specimen from the Morgan Limestone. One *E. geelongensis* individual, from Western Victoria, has part of the outer shell, the septa and the siphuncle preserved in the unaltered state. External moulds of a few individuals are available.

The internal moulds are mostly phragmocones, either distorted or unaffected by diagenesis. However the less easily preserved living chambers are often found. Thus any breakage which occurred usually resulted in loss of varying amounts of the living chamber wall, and all other deformation was post-sedimentational.

Worm tubes occur, preserved as furrows in the surface of the internal mould. One *E. geelongensis* individual (spec. F15560) however has several moulds raised above the surface of the internal mould of the living chamber. These were formed in the shell wall, although not completely enclosed by the latter. It is not clear whether they have been closed at least partly by carbonate of the worm's own secretion, or whether the worm formed no tube, but merely gouged out a furrow in the shell of the (dead) nautiloid. The other accessory organism affecting preservation is the sponge *Cliona*, borings of which are found in a specimen of *E. altifrons*.

The material from Western Victoria consists of fragmentary, unaltered shell of *E. geelongensis* individuals, the matrix being an unconsolidated, richly fossiliferous marl.

(b) *Eocene Species.*—Most individuals of *C. felix* are more or less distorted internal moulds. Those from the Tortachilla Limestone include undistorted specimens. Several specimens from the Blanche Point Marls on the coast have much of the shell remaining and essentially unaltered. These are laterally flattened, whereas others from the equivalent beds at Happy Valley are not so crushed, but without any original shell. Distortion occurred after infilling.

Worm furrows and encrusting Bryozoa are found on those from the coastal localities. Furrows occur both on the internal moulds and in the shell itself. In the former case the worms lived inside the shell, either during the life of the nautiloid or more probably after its death. The worms which made the furrows in the original shell, lived in the outer parts of the test and, here also, may have been present while the nautiloid was alive.

Silicification of the matrix of *C. yorkensis* also resulted in preservation of septa and other parts of the phragmocone in both specimens. Otherwise the latter are well preserved internal moulds.

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JOURNAL OF PALEONTOLOGY, V. 33, NO. 3, P. 449–450, PL. 67, MAY 1959

THE BACULUM OF THE MIOCENE CARNIVORE *AMPHICYON*

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ABSTRACT—A complete baculum of *Amphicyon* is figured and compared with similar elements found in *Ursus* and *Canis*.

INTRODUCTION AND ACKNOWLEDGMENTS

COMPLETE skeletons of Miocene carnivores are conspicuous by their absence in museum collections and those few that are known, having heterotopic bones preserved, are rarer still. One unusually complete specimen, with the baculum present, became known to the writer during the course of the recent study of the postcranial skeleton of *Amphicyon* from the Florida Miocene (in press). This specimen, *Amphicyon sp.* U. C. 36279, is from the Miocene of Colorado and is contained in the collections of the University of California.

Since it is an established fact that the structure of the baculum is of taxonomic importance in determining between species or genera within a family, at least in some smaller carnivores and rodents, it is worthy of recording and figuring this unique specimen in the event that more material of this sort may turn up and be used in morphologic studies of a similar nature in these larger Miocene carnivores.

The affinities of *Amphicyon* have been discussed as being with either the *Canidae* or the *Ursidae*, depending upon the taste of the describing author. Comparable bones of representatives of these two families have been referred to and figured in the comparison of the Miocene specimen (Pl. 67, figs. 1–3).

Thanks are due Dr. D. E. Savage, of the University of California, for permission to describe this element and to Dr. W. H. Burt, of the University of Michigan, for allowing the writer to compare similar bones from the collection of recent mammals that are a part of that institution's reference material.

DISCUSSION

The baculum of the domestic dog has been discussed by most writers dealing with the anatomy of this animal and detailed sections of the reproductive organ are figured by Miller (1952). The *os priapi* of the bear and *Amphicyon* have been more or less omitted from the descriptions of these two forms. The heterotopic bone in *Daphoenodon*, the closest related genus to *Amphicyon*, has been figured and briefly described by Peterson (1910). However, some confusion exists as to his interpretation of the features of this bone in *Daphoenodon*. The trough or urethral groove, located on the ventral side of the baculum is described by Peterson as occupying the superior or dorsal surface of this bone. This groove is normally situated on the ventral face to receive the urethra, the dorsal surface being capped by the erectile tissue of the glans. If, as Peterson states, this groove in *Daphoenodon* is located on the opposite side from that of other carnivores its purpose and function are not at all clear. The groove, as found in *Amphicyon*, forms a trough on the ventral face of the distal end of the bone. A lensiform opening, whose function is not known, pierces the bottom of this trough near its apex. Openings, of a similar sort, were not found in any of the bones that were examined and compared with the Miocene example. The distal end of the baculum, identified as belonging to *Daphoenodon*, terminates in a bifurcate apex rather than the fluted end found in *Amphicyon* or the rounded ends present in *Ursus* and *Canis*. The ventral surface of this element in *Ursus* does not possess a groove for the urethra being instead a flattened or sometimes slightly concave surface. This same face in *Canis* has a deep urethral groove beginning at the base of the element and blending with the rod shaped terminus of the bone. The bases of all of the compared forms exhibit rugose areas indicating a strong muscle attachment. In the dog at least the baculum is

contained in the glans portion of the organ but whether or not this was true in the fossil forms cannot be determined by the preserved portions alone. *Amphicyon* does not possess the crest, for attachment of the glans, on the dorsal surface of the baculum as does the bear and dog. It is instead a rounded surface having a restriction in that area containing the urethral groove.

The skeleton of *Amphicyon* U. C. 36279 is that of an old individual of considerable size, the baculum being much larger proportionally than that found in either the bear or the dog.

No specimens of this element have turned up in the Florida quarries of Miocene age, but on the evidence of the abundant skeletal remains of this large carnivore that have been recovered from the Thomas Farm dig in recent years, it is hoped that heterotopic bones of this animal will be recovered, with the possibility of being used in a taxonomic study and comparison of these specimens with those of the more recent carnivores.

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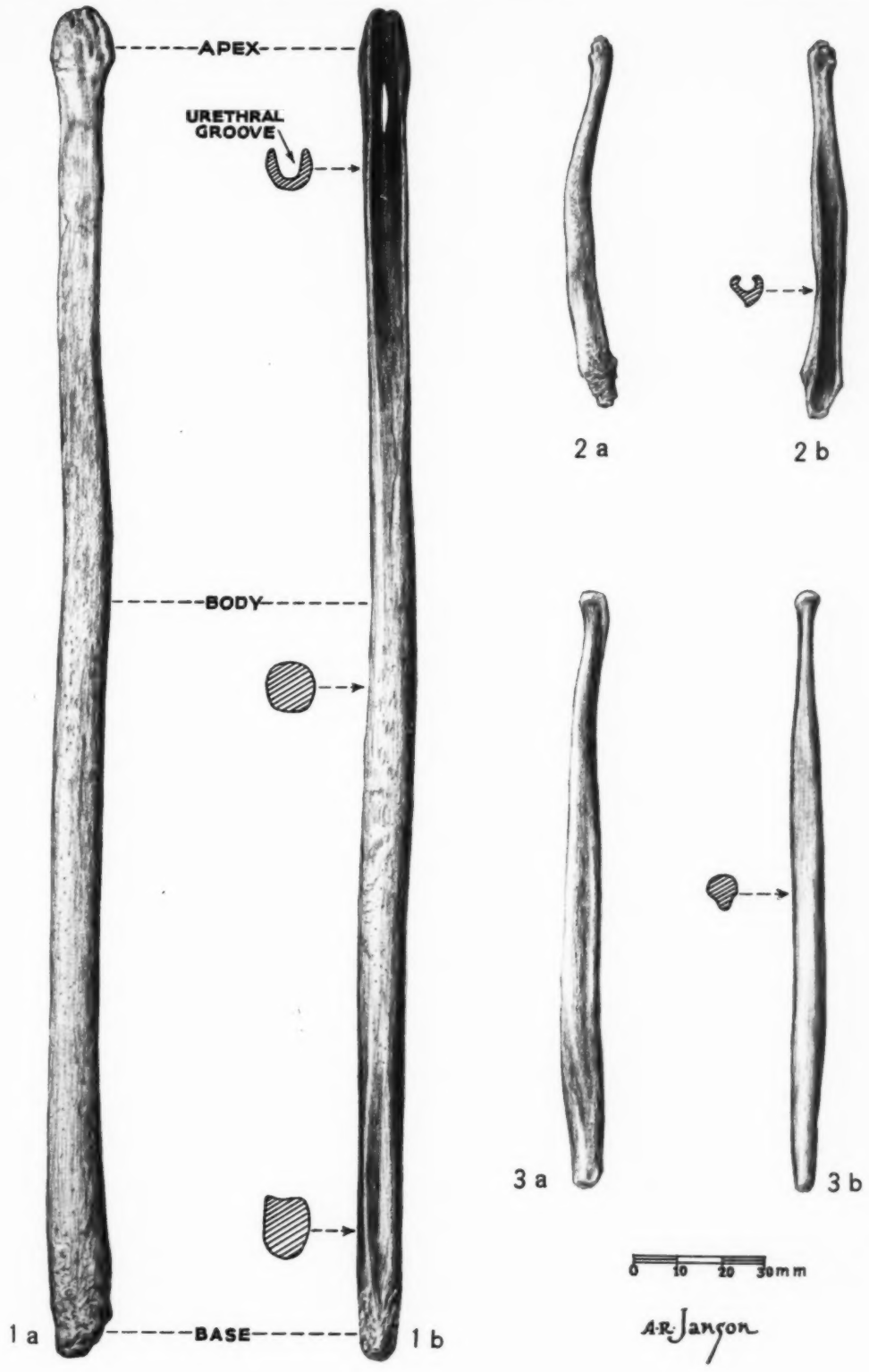
MANUSCRIPT RECEIVED SEPTEMBER 18, 1958

EXPLANATION OF PLATE 67

FIG. *1—Amphicyon sp.* a, lateral view; b, ventral view of baculum, U. C. 36279
2—Canis familiaris. a, lateral view; b, ventral view of baculum.
3—Ursus americanus. a, lateral view; b, ventral view of baculum.
Cross sections shown as hatchures.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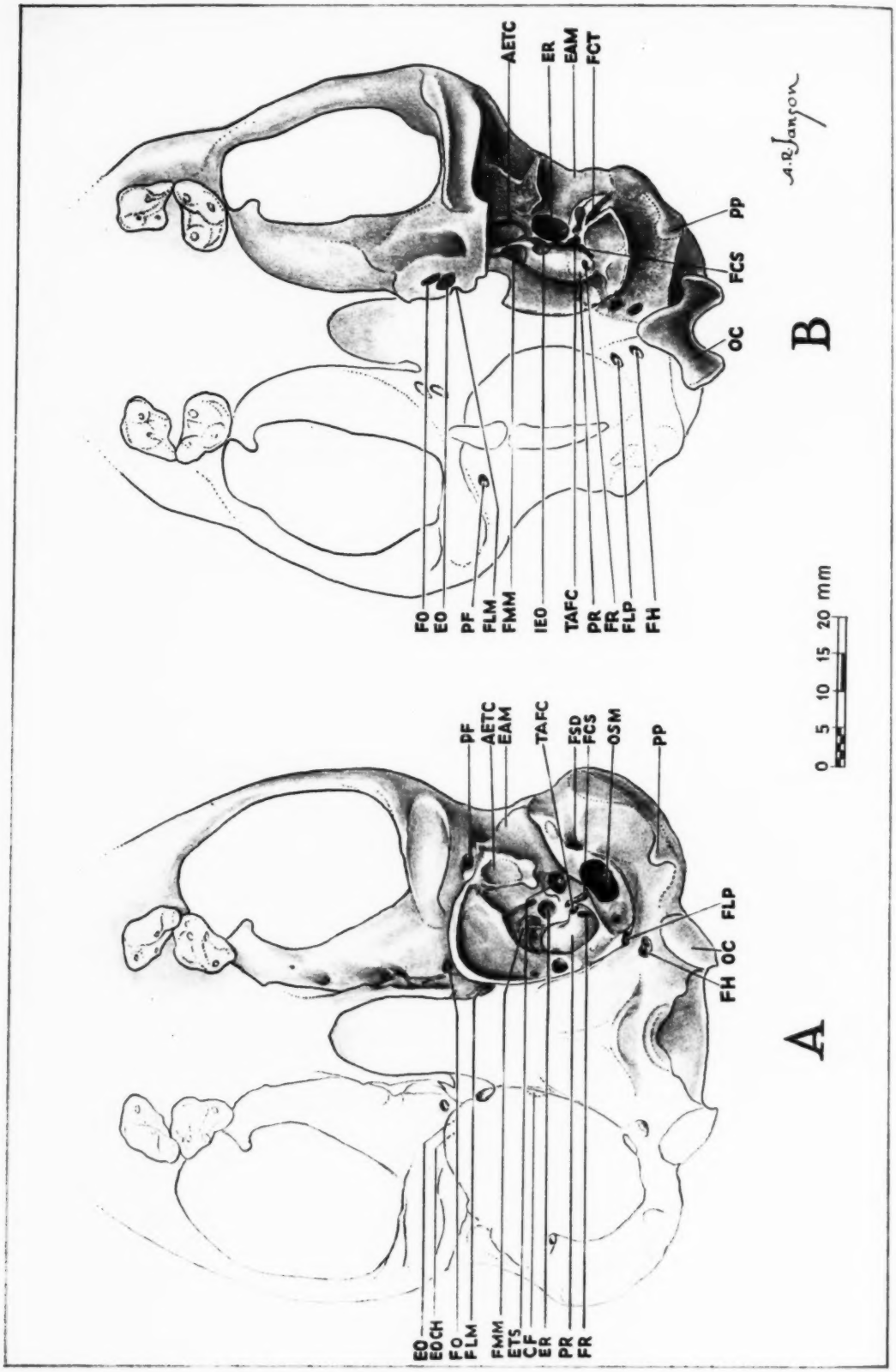
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JOURNAL OF PALEONTOLOGY, V. 33, NO. 3, P. 451–452, PL. 68, MAY 1959

THE MIDDLE EAR OF THE MIOCENE MUSTELID *LEPTARCTUS*

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ABSTRACT—A figured description of the middle ear of the mustelid *Leptarctus ancipidens* from the Florida Miocene. This form is compared with the badger *Taxidea taxus*, the closest living related form.

INTRODUCTION AND ACKNOWLEDGMENTS

ONLY three skulls of *Leptarctus*, known to the writer, have the ear regions sufficiently preserved to warrant a close comparison with the skulls of the better known related mustelids. In one of these specimens, F.G.S. V-5706, the floor of the tympanic cavity and a portion of the middle ear were complete enough to merit a brief description by the writer (1958). During the summer of 1958, a field party of the Florida Geological Survey recovered two additional partial skulls of *Leptarctus ancipidens* from the Thomas Farm Quarry, located in north central Florida, and these specimens form the basis for this present study.

The value of the auditory region, as an aid to classification, has been discussed by many previous writers and in particular by Hough (1944, 1948) and Segall (1943). Since many of the morphological features of the skull and dentition are closest to those found in the badger *Taxidea taxus*, skulls of this recent carnivore were used in the comparison of *Leptarctus*.

I wish to thank Prof. Bryan Patterson of the Museum of Comparative Zoology at Harvard for this helpful discussions relating to the otic region in these mustelids. However, I take full responsibility for any statements made in this contribution that may not be in agreement with those of Prof. Patterson. Miss Barbara Lawrence, also of the Harvard Museum, as well as Dr. R. Van Gelder of the American Museum of Natural History, and Dr. W. Burt of the University of Michigan were most kind in making available the recent material referred to in this paper.

SYSTEMATIC DESCRIPTIONS

Family MUSTELIDAE
Subfamily LEPTARCTINAE
Genus LEPTARCTUS
LEPTARCTUS ANCIPIDENS

Horizon and locality.—Lower Miocene, Thomas Farm Quarry, Gilchrist County, Florida.

Material used for comparison.—Nearly complete skulls of *Leptarctus ancipidens*, F.G.S. V-5834 and V-5706, plus a fragmentary skull exhibiting the right otic region and containing the middle ear, F.G.S. V-5833. Three dried and cleaned skulls of the badger *Taxidea taxus*, with auditory ossicles in place, were sectioned as was a preserved head of an immature badger.

Discussion.—The most apparent differ-

EXPLANATION OF PLATE 68

FIG. *A*—*Taxidea taxus*. Ventral aspect of left otic region (tympanic removed).
B—*Leptarctus ancipidens*. Composite restoration of ventral aspect of left otic region tympanic removed).

Abbreviations are as follows: AETC, anterior expansion of tympanic cavity; CF, carotid for.; EAM, external auditory meatus; EO, eustachian opening; EOCH, external opening of canal of Hugier; ER, epitympanic recessus; ETS, entrance to sinus; FCS, facial canal second part; FCT, facial canal third part (section); FH, for. hypoglossi; FLM, for. lacerum medium; FLP, for. lacerum posterium; FMM, fossa muscularis major; FO, for. ovale; FR, fenestra rotundum; FSD, for. stylomastoideum definitivum; IEO, internal eustachian opening; PF, postglenoid foramen; PR, promontorium; OC, occipital condyle; OSM, opening into sinus in mastoid; PP, paroccipital process; TAFC, tympanic aperture for facial canal.

ence between the otic region of *Leptarctus* and that of *Taxidea* is the greatly enlarged mastoid area and the inflated bullae of the latter. There are two large sinus cavities present in the ear region of the badger which are not found in *Leptarctus*. The largest of these cavities is contained in the mastoid process and is in communication with the posterior part of the tympanic cavity through an opening located in a posterolateral position from the promontorium. The second air space is situated above the auditory meatus and connects with the tympanic cavity at the lateral margin of the epitympanic recessus. This latter fossa receives the head of the malleus. The epitympanic recessus is proportionally larger in *Leptarctus* than that which is present in *Taxidea*.

The fossa muscularis major is represented by a roughened area in *Taxidea* but is a plainly visible pit in *Leptarctus*. The promontorium in the badger is set at an angle, directed in a posterolateral direction, from the long axis of the skull, whereas this same element in the Miocene form is nearly parallel with this axis. Both animals have a well defined fenestra rotundum piercing the posterior end of the promontorium. The eustachian canal opens into the tympanic cavity of the badger from a position just anterior to the fossa muscularis major, exhibiting no perceptible osseous tube or canal after it enters the tympanic cavity. In *Leptarctus* this same opening continues into the tympanic cavity through a groove, and in part a tube, which passes the fossa muscularis major at its lateral edge to terminate in a pit at the anterior end of the promontorium. The anterior expansion of the tympanic cavity is of nearly the same relative proportions in both forms. The tympanic aperture for the facial canal is well defined and is situated immediately above the fenestra rotundum in both animals. The opening of the canal of Hugier is nearly hidden by the anterior swelling of the bulla but its position is established, in the badger at least, as being located in a lateral position to the eustachian opening with a thin wall of bone separating the two foramina. The canal of Hugier has not been identified in *Leptarctus*, due to the crushed and cracked condition of this area in the fossil material. The second part of the facial canal is located in a posterior position to the tympanic aperture with a thin wall separating these two canals. This arrangement is the same in both the recent and the fossil badgers. The third part of the facial canal in *Leptarctus* is destroyed at its external terminus but joins the other parts of the facial canal through a heavy walled tube as evidenced by the only specimen having this area exposed in a broken fashion (F.G.S. V-5833). Both the external eustachian opening and the foramen ovale are situated well ahead of the tympanic bullae and medially to the glenoid fossa in *Leptarctus* whereas these foramina are located at the anteromedial face of the bulla and in a posterior position to the glenoid fossa in *Taxidea taxus*. The foramen lacerum posterium is present at the posteromedial margin of the bulla in both forms with the foramen hypoglossi piercing the skull in a position posteromedially to this first named opening.

The external auditory meatus in the badger enters the tympanic cavity at a definite anterolateral angle to the midline of the skull as compared with a more or less right angle with the sagittal plane as exhibited in *Leptarctus*.

There is a great variation in the degree of inflation of the bullae and whether or not sinus cavities are present in the living genera of Mustelidae. Just why the skull of *Leptarctus*, which is so closely comparable to the badger in most respects, does not have a sinus or inflated bullae cannot be explained from the known material of this most interesting Miocene carnivore.

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THE FOSSIL FLORA OF IPOLYTARNÓC

(Preliminary Report)

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ABSTRACT—Leaf and fruit remains from the upper level of a sandstone showing high glauconite content and from the rhyolitic tuff lying immediately upon it, found in Ipolytarnóc (Northern Hungary) are described; there are 10 new species and a new combination: *Lobaria jablonszkyi, Anacolosa protofrutescens, Kadsura protowightiana, Magnoliaestrobus hungaricus, Scolopia protoluzonensis, Schefflera gaudini* n. comb., *Schefflera protomicrophylla, Schefflera protolucescens, Schefflera protomulticaulis, Antholithes araliaeformis, Tricalysia protojavanica.* The recent relatives of the fossil plants described live in the mountain regions of Southeastern Asia, scattered in rain forests. It is probable that the plants which lived in Ipolytarnóc, required a similarly high humidity and warm temperature. As it may be inferred from investigations embracing the whole fossil flora of Ipolytarnóc, its age is Upper Oligocene.

INTRODUCTION

TOPOGRAPHIC AND GEOLOGIC CONDITIONS

IPOLYTARNÓC is situated in Northern Hungary, Nógrád County, on the left bank of the river Ipoly, latitude 48°15′ North and longitude 19°40′ East. A few kilometers east of the village a ramified valley-system cuts into hills 200–330 m. above sea level. These hills are composed for the most part of sandy clay sediments, conglomerate, a sandstone of very high glauconite content (the so-called "sandstone with the footprints") overlain by gray or white biotitic rhyolitic tuff. Marine sediments of the whole valley-system are members of the Oligocene series (Noszky sen., 1930–31).

The sandstone has a rich fauna, with littoral mollusks, oysters and a very great number of shark teeth. Most of the shark species ranged over Europe from the Eocene through the Middle Miocene (Koch, 1903). Vertebrae of sharks and the caudal vertebra of a *Delphynus* sp. were also found. On the surface of the glauconitic sandstone footprints of primeval mammals: pachyderms, deer-like animals with paired toes and birds were found (these are not yet satisfactorily determined) and here lived also those plants which were buried by the rhyolitic tuff of a volcanic outburst.

The opinions of experts differ as to the age of the sandstone. The age of the glauconitic sandstone with the footprints in the opinion of the mammalogists is Lower Miocene (Tasnádi-Kubacska, 1958). In the opinion of geologists the glauconitic sandstone belongs to the Oligocene (Böckh, 1905; Ferenczi and Horusitzky, 1940; Noszky sen., 1943), while the rhyolitic tuff, which at Ipolytarnóc is situated directly above the glauconitic sandstone, may be classified as belonging to the Lower Miocene (Aquitanian) Noszky sen., 1930, 1943). According to other opinions the rhyolitic tuff, also belongs to the Upper Oligocene as a terrestrial layer concluding a cycle (Bartkó, 1948, 1952); its lower part contains the richly fossiliferous strata.

The rhyolitic tuff that might have fallen in several phases, has a thickness of 0–50 m. Its uppermost and thickest layer is barren, without any trace of organic remains. The average altitude of the fossiliferous layer is 273 m. above sea level. Petrographic and chemical analyses show high glauconite content in the "sandstone with footprints" which turns into a type called glauconitic quartz sandstone. Binding substance of the former is opal, of the latter chalcedony.

The upper level of the glauconitic "sandstone with footprints" and the rhyolitic tuff with the plant remains embedded in it form a biostratonomic unit and it is impossible to draw a geologic boundary line between

them. The plants embedded in the rhyolitic tuff show that they belong to the vegetation which lived before the volcanic outbursts. Whatever artificial time scale may be applied to fix the geologic age of the rhyolitic tuff, that does not change either the character nor the position of the flora. In my opinion the age of the flora is at the highest Upper Oligocene, as may be inferred from the fossil plants.

THE FOSSIL PLANT REMAINS

It seems certain that the plants of Ipolytarnóc were autochthonous, i.e., they lived where they were buried. About 5000 plant specimens were studied, for the most part leaf impressions. The collection contains few impressions of fruits and flowers. Trunks of trees of considerable size and pieces of silicified wood are scattered over the territory.

LIST OF FOSSIL SPECIES

Lichenes:
Lobaria jablonszkyi n. sp.
Bryophyta:
Muscites sp.
Filicinae:
Woodwardites roessnerianus Ung.
Asplenium sp.
Lastrea stiriaca (Ung.) Heer
Dryopteris kümmerlei Jabl.
Coniferae:
Pinuxylon tarnocziense (Tuzson) Kräusel
Pinuphyllum sp. (3 needles)
Pinuphyllum sp. (5 needles)
Pinustrobus sp.
Heyderia salicornioides (Ung.) n. comb.
Heyderiaestrobus salicornioides (Endl.) n. comb.
Palmae:
Calamus noszkyi Jabl.
Sabal major Ung.
Sabal haeringiana Ung.
Licuala sp.
Araceophyllum sp. div.
Araceospadix sp.
Liliaceae:
Smilax obtusifolia Heer
Smilax franklini Heer
Smilax sp. div.
Piperaceae:
Saururus sp.
Piper sp.
Juglandaceae:
Pterocarya denticulata (Web.) Heer
Myricaceae:
Myrica lignitum (Ung.) Sap.
Fagaceae:
Quercus oligodonta Sap.
Quercus armata Sap.
Quercus cruciata A. Br.
Quercus neriifolia A. Br.
Castanopsis toscana (Bdlk.) Kr. et Wld.
Castanopsis sp.
Moraceae:
Ficus persephones Etth.
Ficus sp. div.
Olacaceae:
Anacolosa protofrutescens n. sp.
Magnolia attenuata Web.
Magnolia dianae Ung.
Magnolia ludwigii Etth.
Magnolia sp. div.
Manglietia sp.
Michelia sp.
Kadsura breddini Wld.
Kadsura protowightiana n. sp.
Kadsura sp.
Talauma sp. div.
Illicium fliegeli Wld.
Magnoliaestrobus hungaricus n. sp.
Magnoliaestrobus noszkyi (Jabl.) n. comb.
Annonaceae:
Polyalthia sp. div.
Orophea sp.
Alphonsea sp. div.
Lauraceae:
Cinnamomophyllum scheuchzeri (Heer) Kr. et Wld.
Cinnamomophyllum polymorphum (A. Br.) Kr. et Wld.
Actinodaphne sp.
Laurus primigenia Ung.
Dehaasia sp.
Lindera styracifolia (Web.) n. comb.
Lindera stenophylla (Etth.) n. comb.
Lindera sp. div.
Litsea magnifica Sap.
Litsea grandifolia (Etth.) n. comb.
Litsea mülleri Friedr.
Litsea sp. div.
Persea sp.
Phoebe sp. div.
Laurocarpum sp.
Lauropetalum sp.
Pittosporaceae:
Pittosporum sp.
Leguminosae:
Dalbergia sp. div.
Leguminocarpum sp.
Antholithes leguminosoides (vexillum)
Aquifoliaceae:
Ilex rottensis Wld.
Celastraceae:
Evonymus sp.
Aceraceae:
Acer trilobatum A. Br.
Sapindaceae:
Sapindus sp.
Xerospermum sp.
Sabiaceae:
Meliosma sp.
Elaeocarpaceae:
Elaeocarpus sp.
Flacourtiaceae:
Scolopia protoluzonensis n. sp.
Scolopiaephyllum sp.

LIST OF FOSSIL SPECIES (*Continued*)

Barringtoniaceae:
Barringtonia sp.
Combretaceae:
Terminalia sp.
Myrtaceae:
Eugenia sp.
Melastomataceae:
Memecylon sp.
Araliaceae:
Schefflera gaudini (Sap.) n. comb.
Schefflera protomicrophylla n. sp.
Schefflera protomulticaulis n. sp.
Schefflera protolucescens n. sp.
Schefflera sp. div.
Macropanax sp.
Acanthopanax sp. div.
Aralia ilicifolia Sap.
Antholithes araliaeformis n. sp.
Myrsinaceae:
Myrsine formosa Heer
Sapotaceae:
Sapotacites delprati Crié
Sapoticarpum sp.
Ebenaceae:
Diospyros brachysepala A. Br.
Diospyros sp.
Diospyros rugosa Sap. (calyx)
Symplocaceae:
Symplocos sp. div.
Oleaceae:
Osmanthus dianae (Etth.) n. comb.
Rubiaceae:
Tricalysia protojavanica n. sp.

PALEOPHYTOGEOGRAPHIC RELATIONSHIPS OF THE FLORA

The fossil flora of Ipolytarnóc shows affinities first of all with the flora living today in the tropical and subtropical as well as temperate mountain regions of southeastern Asia: the southern slopes of the Himalaya, South China, Assam, Burma and Malaysia. A smaller number of species could be related to plants living now in the Atlantic and Gulf States of North America and only a few with those living on the Canary Islands and around the Mediterranean Sea.

The flora might have belonged to different formations of a tropical-subtropical vegetation. The overwhelming majority of tropical genera and the very frequent occurrence of some of their species, however, gives to this flora a rather tropical cast. The most typical picture which may be ascertained from this flora, is a dense tropical rain forest, with a subtropical character. The species seem to have been grouped into associations probably differing from those of today. In Ipolytarnóc there were mostly hydromegatherm and mesotherm plants requiring high humidity and a high temperature. This is proved by the prolonged, slender acumens of leaves frequently met with, by their relatively large, leathery, partly entire-margined and partly dentate blades and by their sparse, wide venation. The growth rings of woods are in general well-defined.

Of the territory whose recent flora has been compared with the fossil flora, Assam shows, e.g., maximum temperatures between 35.5°–43.3°C., minimum temperatures between 5.5°–15.5°C. and the annual precipitation amounts to 1016–3810 mm. At the foot of the Himalaya the annual mean is 20°C., i.e., 5° below that of Assam. I compared the vegetation of Ipolytarnóc with a recent flora living in a broad territory within the same floral realm of the Assam-Himalaya region and this shows the greatest floral resemblance. We may therefore assume that the plants of Ipolytarnóc might have likewise required an annual average mean of 20–25°C. and an annual precipitation ranging between 1016–3810 mm. Besides hydromegatherm and mesotherm plants stenotherm genera were also present, pointing to a temperate mountain flora.

The paleogeographical situation of Ipolytarnóc supports favorably these inferences. Besides the proximity of the seashore, a warm Tertiary current from the Indian Ocean towards Southern Europe of these days might have contributed a warm-humid, maritime climate to the vegetation which seems to have lived in part near the shore (Schwarzbach, 1950). In which zones of altitude the mountain flora adduced for comparison, might have lived in Ipolytarnóc relative to the sea level of those days, I cannot say; one must take account, on the one hand, the possibility that the territory of Ipolytarnóc, or part of it, was then more elevated than today and, on the other hand, it may be that a mountain flora of our days lived in Ipolytarnóc as a lowland flora. Furthermore it is very probable that the vegetation could thrive for a longer time undisturbed on the emerged territory, an as-

sumption proved by the survival of relict species. Genetically this vegetation can be connected only with that which lived in the preceding geologic age in the surrounding region. The volcanic catastrophe put a sudden end to this flora over a wide-spread territory.

The findings at Ipolytarnóc prove the presence of several, now discontinuous genera in the Tertiary (Upper Oligocene) of Europe. These formed therefore a link between the genera living today in Southeastern Asia on the one hand and those living in North America on the other.

SYSTEMATIC DESCRIPTIONS

LOBARIA JABLONSZKYI Rasky n. sp.
Pl. 69, figs. 1,2

Impressions of various sized pieces of a thallus of lichen of leaf-like structure, usually jumbled forms. At certain places the impressions have large, lobed borders. The surface of the thallus of lichen is of reticulated structure, having a pitted surface, the diameter of the pits being in the order of 1 to 8 mm. At the lower side, corresponding to the pits the thallus is embossed or gnarled. The gnarls are separated by striae. The pits or gnarls are irregularly circular or ellipsoid, or occasionally angular. The distribution of the smaller or larger pits or gnarls is wholly irregular and without system. There are neither rhizoidae, nor remnants of apothecium on the thalli of lichen.

So far about 50 specimens of the species *Lobaria jablonszkyi* have been found. At Ipolytarnóc the finds are by no means rare. Jablonszky (1914:266) already observed the occurrence of this cut-up, laminated fossil, and in his work he refers to it as a remnant of uncertain position. There are no definite data of Tertiary lichens, which may be used for comparison.

It may best be compared to the *Lobaria retigera* (Bory) Nyl. of recent lichen species. It may be found on mossy rocks and trunks and may develop into large thalli. This lichen still survives in the tropical regions of southeastern Asia.

Anacolosa protofrutescens Rasky n. sp.
Pl. 69, fig. 3

Oblong, entire-margined leaves. They have a short attenuated apex, the base being slightly decurrent. In the upper third the leaf expands only slightly. The length of the leaves is 15 cm., their width being 6 cm. The midvein is thick, tapering towards the apex. The secondary veins are relatively thin and curved. There are 6 to 7 pairs of secondaries starting alternately and not very regularly spaced (1.0–1.5–2.0 cm.), from the midvein. The first pair of secondaries at the base of the leaf is short, running upwards almost parallel to the margin. From the third or fourth pair of secondaries on the veins run to the margin of the leaf, curving immediately before the margin almost in a right angle, and thereafter continuing alongside the margin to the apex. No other venation or reticulation is visible on the remnants.

Other genera of the family Olacacea are from the Lower Eocene age (London Clay) present in Europe and in North America also (Wilcox group).

With their characteristic secondary veins the impressions compare well to the leaves of the *Anacolosa frutescens* Bl. found in Java. Bushes or trees extending to heights of 1000 m. above sea level. The species is rather frequent in rain forests; it may be found dispersed.

KADSURA PROTOWIGHTIANA Rasky n. sp.
Pl. 69, fig. 6

Oval, entire-margined leaves, their length being 8.5 cm. their width 4.5 cm. From the relatively wide leaf the apex rises abruptly, ending in a short acumen. The base is only slightly decurrent. The remnant of the petiole is 1 cm. long. The midvein is well visible, while the 7 to 9 parallel secondary veins, slightly turned upwards, are rather faint. The secondary veins are camptodrome, connecting in regular loops at the margin of the leaves. No traces of a tertiary venation or meshwork are visible.

The leaves of the *Kadsura protowightiana* differ from those of the *Kadsura breddini*, the latter being described by Weyland (1934:68), in Germany from the Oligocene of the Lower Rhineland (Kreuzau). No morphological comparison is possible between the remnants of Ipolytarnóc and the leaves of the *Kadsura senftenbergensis* Jähn. and *Kadsura lusatica* Jähn. species, these being known only from small fragments. However, their original organic substance has

been preserved, so that the species could be determined by way of cuticular analysis and compared to recent *Kadsura oblongifolia* Merr. and *Kadsura hainanensis* Merr. species (Jähnichen, 1954).

Leaves of a shape and venation similar to the Ipolytarnócian impressions may be found on the still surviving *Kadsura wightiana* Arnott. The secondary veins are only faintly visible even on the recent species. In Ceylon the species extends on mountain sides to heights of 600 to 900 meters. On recent species leaves entire margined or toothed may occur promiscuously.

MAGNOLIAESTROBUS HUNGARICUS
Rasky, n. sp.
Pl. 70, figs. 7,8

The impressions of the fruits are either spheroid or oval. The length of the largest specimen is 3.5 cm., its width being 2.5 cm. The fruit, several carpella scarcely expanding in the middle, is arranged spirocyclically on the spathe. The measurable length of a carpellum being 1 cm., its maximum width 0.6 cm. On the remnants the apices of the carpella are broken off. Along the carpellum there is a scutum. The stamina bearing part of the spathe is relatively long, its length being 3.5 to 4 cm. on the fossils, its width 1 cm. The cicatrices of the stamina also appear to be spirocyclically arranged on the remnants of the spathe. The hardly expanding base of the spathe, the cicatrices of the perianthium, show large, oval or penta-, or hexagonal impressions. As compared with the number of the stamina there are only a few impressions, their arrangement being annular. There is no internodium between gynoeceum and stamina on the spathe. The fruits are unripe, the carpella being unopened upwards. Impressions of more than 10 fruits have been found, part of them still retaining the portion of the spathe bearing the stamina.

These fruits may be allotted to the genus *Magnoliaestrobus*, a genus first described by Seward and Conway (1935). However, the fruits of the Cretaceous *Magnoliaestrobus gilmourii* Sew. and Conw. are considerably larger than those found at Ipolytarnóc. As compared with the Ipolytarnócian remnants the fruit of the *Magnolia inglefieldii* Heer (1870) has a rather elongated form. As regards size and shape the fruit of *Magnolia ludwigii* Etth. (1868) known from Salzhausen comes close to the Hungarian find, the part of the spathe bearing the stamina being narrower and shorter. The badly formed fruit cannot be identified to the Ipolytarnócian specimen. The fruit of the species known as *Magnolia sigmaringensis* (Quenst.) Kirchh. of the German Tertiary is considerably larger, the carpella being wider, the staminous part of the spathe narrower and shorter, the portion bearing the perigonium contracted and tapered, so that this find cannot be identified with the Ipolytarnócian specimen. As may be seen from the reconstruction of Kirchheimer (1954, Pt. 4) also, the fruits are widely different from one another.

By far smaller specimens of fruit have also been found at Ipolytarnóc, having narrower carpella, with narrow, yet long stamina bearing spathe rests. The spathe remnants are, however, frequently missing. Already Jablonszky described a fruit (1914: 236:9:2) from Ipolytarnóc where the stamina bearing portion of the spathe was missing. He believed it to be a palm fruit and described it as *Calamus noszkyi* Jabl. common for palm leaves. These may be segregated as *Magnoliaestrobus noszkyi* (Jabl.) n. comb. from the larger fruits. These fruits cannot be brought into relation with the fruit of the fossil palm *Calamus*, described by Chandler (1957) from the Oligocene.

It is difficult to establish a closer relationship with recent species. Certain *Talauma* and *Magnolia* species have stamina bearing spathe portions as regards length and thickness approximating those of the fossil species. However, the form of the carpella on these species differs from that of the Ipolytarnócian find. The genus *Michelia* may be discarded owing to its internodium. However, there are undoubted ties with the Magnoliaceae family.

SCOLOPIA PROTOLUZONENSIS Rasky n. sp.
Pl. 70, fig. 9

Oblong leaves of variable size. The apex being more or less acuminate, the base gradually decurrent. On the margin of the leaf widely spaced obtuse or occasionally acute teeth may be found. The length of the leaves is 8 to 10 cm., their width being about 4 cm.

The midvein is strongly expanded towards the base. At the base two pairs of secondary veins ascend from the midvein. The outer basal pair is thinner and borders the inner thicker pair of basal secondaries with narrow, long loops. The further 4 pairs of secondaries start alternately from the midvein, at distances of about 1.5 cm. These secondaries tend rather to the margin of the leaf, where they connect in large, irregular loops. These secondaries often run in broken, and not in straight lines. The large loops are at the margin of the leaf and are bordered by smaller loops from which short veins start to the teeth. The tertiary veins form a spacious meshwork. Besides the leaf is interwoven by a less spacious fine meshwork of veins. Texture is coriaceous.

The remnants compare favorably to the leaves of the recent species of *Scolopia luzonensis* (Presl.) Warb., the home of this species being the Philippines.

SCHEFFLERA GAUDINI (Sap.) n. comb.
Pl. 70, fig. 12

Oblong or lanceolate, entire-margined leaves, base and apex missing. The measurable length of the leaf on the remnants is 8 to 9 cm. (its real length was presumably 15 to 17 cm.). The width is about 4 cm. There are no remnants on the petiole. The leaf does not expand, the margin being parallel to the midvein. The midvein is thick, the secondaries thin, yet well visible. The short, parallel secondaries start from the midvein at distances of 1.0 to 1.5 cm. There were presumably 10 to 12 pairs of secondaries on the entire leaf. The secondary veins are furcate and connect in a characteristic acute angle long before the margin. This acute angle is occasionally flattened by a vein running parallel to the margin of the leaf. Besides the acute loops there are other smaller ones connecting the secondaries before the margin of the leaf. The leaf is interwoven by a spacious polygonal meshwork, a finer, less spacious meshwork being visible within the previous one. The leaf is coriaceous (on the entire leaf the base was presumably rounded off, the apex ending in a short acumen).

Saporta (1863:4:19:77:9:3) was the first to describe the *Schefflera gaudini* leaves from finds in Oligocene stratum in Southern France (Aix), as *Aralia gaudini*. He compared them with other recent *Aralia* species partly in Central America, partly in Java. Both the French and the Hungarian remnants of the *Schefflera gaudini* leaves may best be compared to those of the recent *Schefflera lucescens* (Bl.) Vig. var. *rigida* (Bl.) Bakh. The species grows as bushes or trees reaching a height of 10 meters. As a rule there are 7 to 10 leaves with petiole at the end of the long leaf-stalk. There are often epiphytes and climbers. The species live today in Java at about 1000 to 2300 meters above sea level. Dispersed, yet not rarely, the species may be found in rain forests.

SCHEFFLERA PROTOMICROPHYLLA
Rasky n. sp.
Pl. 69, fig. 4

Oblong, entire-margined leaves, expanding at the center. The length of the leaves is 3.5 to 4 cm., their width being about 1 cm. The base is decurrent, the apex being long attenuated (often broken off on the impressions). Petioles are not visible. The midvein protrudes, secondary veins start from it alternately and sparsely. The lower secondaries are directed to the apex, there being on

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EXPLANATION OF PLATE 69

FIGS. *1–2*—*Lobaria jablonszkyi* Rasky n. sp., somewhat enlarged. Collect, no. 55.549.1. and 58.19.1
3—*Anacolosa protofrutescens* Rasky n. sp. Collect. no. 58.6.1.
4—*Schefflera protomicrophylla* Rasky n. sp. Collect. no. 58.12.1.
5—*Schefflera protomulticaulis* Rasky n. sp., leaf basal fragment, enlarged. Collect. no. 58.13.1 and 58.17.1.
6—*Kadsura protowightiana* Rasky n. sp. Collect. no. 58.7.1.

All type and figured specimens are in The Paleobotanical Collection, Department of Botany, Hungarian National Museum, Budapest, Hungary.

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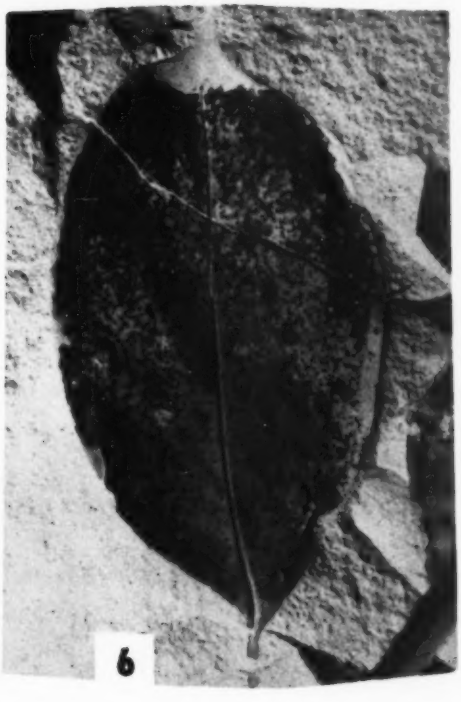
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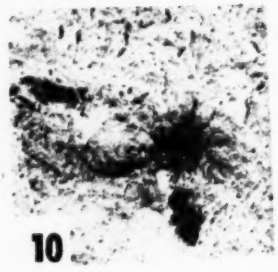
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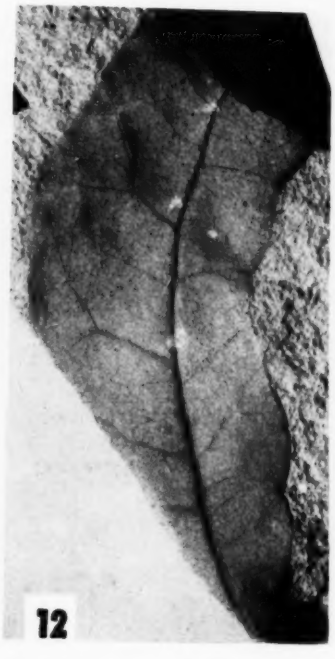
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the whole 4 or 5 pairs of them. The ascending secondaries are camptodrome, connected with each other. In the upper third of the leaf the secondary veins are more densely arranged. A relatively spacious polygonal meshwork enclosed by prominent, well distinguishable veins fill the leaf. Texture coriaceous.

As regards shape the leaves of *Schefflera protomicrophylla* resemble those of the *Cinnamomum;* however, owing to their different venation, the two species are easily distinguishable. The three basal veins do not occur in the *Schefflera protomicrophylla* leaves.

A relationship may be established between these leaves and those of the recent *Schefflera microphylla* Merr. found today on the Philippines (Luzon).

SCHEFFLERA PROTOMULTICAULIS
Rasky n. sp.
Pl. 69, fig. 5

The fragment is 2.5 cm. long and has a fragmentary petiole of 1.5 cm. The remnant is a characteristic base of the oblong, slightly oval, entire-margined leaves. The petiole and the midvein are fairly thick. The upper end of the petiole is cross-wrinkled. At the base, further from the petiole two pairs of thinner secondaries start upwards, parallel to the margin of the leaf. The outer basal pair of secondaries joins the inner basal pair of secondaries with a flat loop. The base of the leaf is also interwoven by a spacious polygonal meshwork, with a finer, less spacious meshwork spreading over it. Texture coriaceous (a perfectly intact leaf of this species has also been found).

The find is comparable to the base of the leaf of the recent *Schefflera multicaulis* Elm. The intact fossil leaf may be compared to this recent species. The species survives today in the Philippines (Luzon).

SCHEFFLERA PROTOLUCESCENS
Rasky n. sp.
Pl. 70, fig. 9

Oblong, slightly oval, entire-margined leaves. The middle part of the leaf expands slightly. The leaves have great variation in size and form. The base is decurrent, the apex is broken off (if extant, it ends in a short acumen). The length of the leaves is 8 to 9 cm., their width being about 3 to 4 cm. The extant portion of the petiole has a length of 1.5 cm. A fine corrugation (cross-wrinkled) appears at the upper end of the petiole. The midvein is relatively thick and tapers towards the apex. From the midvein 6 to 7 pairs of secondaries start alternately, tending upwards and are by far thinner than the midvein. The secondaries are more or less parallel with one another. At the base two pairs of thinner secondaries start from the top of the petiole. The outer pair runs directly alongside the margin and does not tend upwards. The secondaries are furcate near the margin, and connect in angular or acuminous loops. Between the furcate branchings smaller or larger loops connect or border the secondaries. In the upper half of the leaf, too, the secondaries expressly tend towards the apex. The secondaries do not run in a straight line; they are frequently broken. The tertiary veins compose a well visible spacious, polygonal meshwork, among which a yet finer, less spacious reticulation is perceptible. Texture coriaceous.

EXPLANATION OF PLATE 70

FIGS. *7,8—Magnoliaestrobus hungaricus* Rasky n. sp., somewhat enlarged. Collect. no. 58.8.1. and 58.9.1.
9—Scolopia protoluzonensis Rasky n. sp. Collect. no. 58.10.1.
10—Antholithes araliaeformis Rasky n. sp., enlarged. Collect, no. 58.15.1
11—Schefflera protolucescens Rasky n. sp. (entire-margined leaf, on its upper part the rock is jagged). Collect. no. 58.14.1.
12—Schefflera gaudini (Sap.) n. comb. Collect. no. 58.11.1.
13—Tricalysia protojavanica Rasky n. sp. Collect. no. 58.16.1.

All type and figured specimens are in The Paleobotanical Collection, Department of Botany, Hungarian National Museum, Budapest, Hungary.

Saporta (1863:4:19:79:9:4) described the leaves of the *Schefflera decaisnaei* under the name of Aralia *decaisnaei* in Southern France, although comparable to the *Schefflera protolucescens*. They differ from the latter in the form of the venation. In the upper half of the leaves of the *Schefflera* (Aralia) *decaisnaei* the secondaries are denser and all form a larger angle with the midvein, on the other hand, with the *Schefflera protolucescens* species this angle becomes gradually smaller towards the apex. Among others Saporta has compared the fossil leaves to those of *Aralia pergamacea* Bl., the current *Schefflera lucescens* (Bl.) Vig. var. *typica* Bakh. The leaves of varying shape, yet of identical venation of the *Schefflera protolucescens* of Ipolytarnóc, on the contrary, compare well to the highly variegated leaf-form of the recent *Schefflera lucescens* (Bl.) Vig. This seems to substantiate the assumption that the variety of shape was existent already in the Tertiary, resp. in the Upper Oligocene.

The recent *Schefflera lucescens* (Bl.) Vig. is a 5 m high tree found in Java, having 6 to 12 composite leaves. The tree lives dispersed in the rain-forests and is often epiphyte. It is fairly frequent in the forests of higher mountainous regions.

ANTHOLITHES ARALIAEFORMIS
Rasky n. sp.
Pl. 70, fig. 10

Impressions of flower and bud remains grouped in small spheroid clusters. The flower resembles berries, their diameter varying between 0.5 and 0.8 cm. The flowers are seated on the ends of more or less thick petioles. The petioles are rigid, their length being 1 or 2 cm., their width about 2 mm. Small impressions resembling petals are perceptible on the margins of the berry-like spheroid impressions, while other berries remind one of unblown buds. The spheroid heads occur one by one only. Nothing else may be inferred from the impressions. So far about 12 specimens of the flowers have been found.

The frequent occurrence of the Araliaceae leaves seems to support the assumption that the spheroid berry-like remnants may be classified as belonging to the family Araliaceae, although there are several other families having similar flowers grouped in spheroid clusters.

TRICALYSIA PROTOJAVANICA
Rasky n. sp.
Pl. 70, fig. 13

Oblong, entire-margined leaves. The apex is more or less elongated, the base gradually decurrent. The length of the leaves is 10 to 12 cm., their width being about 4.5 to 5.0 cm. No remnants of a petiole are visible. The midvein is strong; there are 6 to 7 pairs of secondaries starting from the midvein, alternately, or oppositely arranged. The starting points of the secondaries are rather apart and the spacings are not uniform, the maximum being 2 cm. The secondaries join in loops of large arcs at the margin followed by gradually decreasing loops. The secondaries are interwoven with a very spacious polygonal meshwork. The leaves are more or less coriaceous.

Remnants of a venation resembling that of the family Rubiaceae compare well to the leaves of the recent *Tricalysia javanica* (Miq.) Kds. These are 15 meter high trees, extending in Java into the mountains to about 500 meters above sea level. They may be found dispersed in light rain-forests.

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PENTECECRINUS, A NEW MICROCRINOID FROM THE LOUISIANA FORMATION OF MISSOURI

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ABSTRACT—A new microcrinoid, *Pentececrinus parvus* (suborder Cyathocrinoidea), from the Louisiana formation (Devonian-Mississippian) of Missouri is described and compared with other nonbrachiate crinoids possessing only three circlets of plates (IBB, BB, OO) and an anal. Such crinoids have been reported from the Mississippian, Pennsylvanian, and Permian of the United States, the Lower Carboniferous of Europe, and the Permian of Timor and Russia. With the addition of *Pentececrinus*, it is inferred that they form a phyletic group extending from late Devonian or early Mississippian to Permian time and that known Permian representatives do not indicate regressive evolution or aberrant specialization.

INTRODUCTION

THE junior author, while studying the ostracode fauna of the Louisiana formation of eastern Missouri early in 1956, extracted from his washed samples approximately 600 calyxes of *Allagecrinus americanus* Rowley 1895. With this wealth of microcrinoid material, he found a unique specimen which he submitted to the senior author for study upon leaving the University of Missouri to join the Creole Petroleum Corporation in 1957.

The specimen is excellently preserved. Its extremely simple thecal structure is unquestionably distinct despite the specimen's small size (height circ. 0.6 mm.). The orals bear characteristic hypertrophic extensions and the dorsal cup is composed of only two circlets of plates and an anal plate. Radial plates are conspicuously absent.

The small number of plates, simplicity of structure, and absence of radials make the specimen comparable with similar types of crinoids presently assigned to the family Hypocrinidae Wanner, 1916 (Bassler and Moodey, 1943; Ubaghs, 1953) or to Codiacrinidae Bather, 1899 (Moore and Laudon, 1943). This ambiguous situation is currently being studied by the senior author for the purpose of necessary revision.

The time range of the phyletic group formed by these related crinoids is now known to extend from the late Devonian or early Mississippian to the Permian. Before now, members of the group had not been reported from formations older than the Lower Mississippian (Osagean) of the United States (Strimple and Koenig, 1956) or the Lower Carboniferous (Viséan) of Belgium (de Koninck and Le Hon, 1854) and of England (Austin and Austin, 1842; Wright, 1952). However, Croneis (1942, p. 1828) in an abstract, announced the discovery of a microscopic crinoid—maximum dimension 0.4 mm. including two stem ossicles—in the Ordovician, Bromide formation, of Oklahoma. He stated that it resembles "in shape, size, and plate arrangement the early nonbrachiate pentacrinoid stage of such modern crinoids as *Composometra*, *Isometra*, and relatives." Because he gives no further description, the relationship of this crinoid cannot be verified at present, but the announcement is mentioned here to indicate the possible antiquity of nonbrachiate forms. The youngest representatives of the group come from the Permian formations of Russia (Yakovlev, 1926), of Timor (Wanner, 1916, 1920, 1924, 1929, 1930, 1937), and of the United States (Girty, 1908).

For almost three-fourths of a century after Austin and Austin (1843) described the species *Sycocrinus jacksoni* (*Lageniocrinus jacksoni*, Kirk, 1940, p. 132), crinoids with calyx structures similar to *Pentececrinus* were the subject of much conjecture and disscussion. In 1854, de Koninck in de

Koninck and Le Hon published a description of *Lageniocrinus seminulum*. Because of its simple structure of just three circlets of plates and lack of arms and even of arm-bearing elements, specimens of the species were considered for a period of 62 years afterwards to be the larvae of some crinoids, specifically of *Synbathocrinus* Phillips, 1836 (Zittel, 1879, p. 350; Wachsmuth and Springer, 1887, p. 99; Springer, 1913, p. 209; and Bather, 1900, p. 152; 1914, p. 249). According to Wachsmuth and Springer (1887, p. 99), de Koninck regarded the tegminal plates of *Lageniocrinus* as radials, but they, like Zittel (1879, p. 350), thought that the plates represented arms which were capable of opening, and that there "were plates underneath covering the calyx." This view obviously was motivated by their comparison of the tegminal plates of *Lageniocrinus* with the corresponding plates of *Haplocrinites* Steininger, 1834 (*Haplocrinus* Roemer) and *Allagecrinus* Carpenter and Etheridge, 1881. In their revision of the Palaeocrinoidea, 1887, they strongly contended, in opposition to Carpenter's views, that the five tegminal plates of these two genera were interradial elements or supplementary pieces which roofed over the underlying, undeveloped summit plates and ambulacral structures (Wachsmuth and Springer, 1887, p. 254). Carpenter (1884, p. 157) had previously compared these two genera to the larvae of *Antedon* Fréminville, 1811 and stated that they are, "permanently in the condition of very early larva." Thus, he believed that the five ventrally situated plates are "oral plates," homologous to the orals of *Antedon* larvae. A somewhat similar opinion had been expressed 20 years earlier by Allman (1864), who compared the oral plates of the larvae of *Comatula* Lamarck, 1816 with the ventral plates of *Haplocrinites* and *Amblacrinus* d'Orbigny, 1849 (*Coccocrinus* Müller). In 1888, Wachsmuth and Springer, in comparing the ventral structure of *Haplocrinites* with a well-preserved specimen of *Taxocrinus intermedius* Wachsmuth and Springer, 1888 (p. 344, pl. 18, figs. 1a-e) reversed their position and accepted the view that the tegminal plates of *Haplocrinites* are orals. They repeated and expanded this opinion again in 1897. This sentiment probably caused Wachsmuth to regard *Lageniocrinus* as a valid genus in 1896 (p. 136), but he still referred it to the Synbathocrinidae S. A. Miller, 1889. In spite of these developments Bather, in 1900 (p. 152) and again in 1914 (p. 249), and Springer in 1913 (p. 209) continued to regard *Lageniocrinus* as a larval form of *Synbathocrinus*. Bather also persisted in referring to the tegminal plates as "first stages of the arms" or first primibrachs. It was not until Wanner (1916, p. 135) recognized the close affinities of *Lageniocrinus* with his new genus *Embryocrinus*, that *Lageniocrinus* was properly placed systematically. Also at that time, Wanner designated the so-called arm plates of *Lageniocrinus* as orals, and he considered the next lower circlet of plates as basals and the lowest circlet of plates as infrabasals. Since then, Wanner's interpretation of the plate structure of this genus and of similar crinoids has been generally accepted.

Discussions concerning morphogeny of nonbrachiate crinoids have been dominated by Wanner since 1920. He summarized his views in 1929 in answer to Yakovlev (1928) who denied the validity of *Lageniocrinus*, explaining it as an abnormality due to arrested development in the ontogeny of any one of several genera. Wanner contended that crinoids without arms and with atrophied radials developed from more complex ancestors, and that this development was accompanied by the displacement of the oral plates from an interradial to a radial position and by the migration of the anal opening from its position in the region of the right posterior ray to the position of the left posterior ray.

Although Wanner's exhaustive arguments appear convincing and have been accepted by many without question, some have questioned his basic premise that nonbrachiate crinoids evolved from more complex forms and thus represent evolutionary degeneracy. The concept was tentatively questioned by Peck (1936, p. 284), and definitely contested by Kirk (1940, p. 138). Both hold that forms like Wanner's Permian *Embryocrinus* are derived from the older Carboniferous genus *Lageniocrinus* instead of the reverse. Discovery of the specimen herein described confirms the contention of Peck and Kirk and extends the range

of this group to possible late Devonian time.

Stratigraphically, the Louisiana formation is considered by some geologists to be Lower Mississippian (Kinderhookian) in age and by others to be Devonian. This controversial issue has been discussed in the literature, and need not be repeated here. The important fact is that *Pentececrinus* is to date the oldest known representative of nonbrachiate, nonradial-bearing crinoids.

Orientation.—Although crinoid orientation (Springer, 1913, p. 175; Moore, 1952, p. 613; Ubaghs, 1953, p. 661) and specifically hypocrinid and (or) microcrinoid orientation (Wanner, 1929, p. 79; Kirk, 1937, p. 111; Moore, 1940, p. 575) has been fully discussed in the literature, it is summarized here to elucidate further discussion.

Conventionally, a crinoid is described in its natural living position with the mouth turned upward. Thus, the ventral or tegminal side is up and the dorsal or basal side, down. Because it lacks a front and back marked by direction of movement, the anus or anal side of the pentamerous form is arbitrarily turned toward the observer. The ray opposite is anterior and right and left correspond to the right and left of the observer. Ubaghs (1953, p. 661) points out that in representation of the dorsal side, the posterior interradius should be turned upward—in illustrations toward the top of the plate or page—and in the case of the ventral side, downward—toward the bottom of the plate or page. In this way the significance of right and left is retained. When the tegminal covering of a crinoid is made up entirely of five plates or orals, it was recognized some time ago (Wachsmuth and Springer, 1888) that the largest of the five lies in the posterior interradius. This plate, as Wanner (1929, p. 79) points out, is also distinguished by its trapeziform outline and by its possession of a pore variously referred to as "?anus +hydropore" (Bather, 1900) "hydropore" (Wanner and authors), and "hydropore? gonopore? or both" (Ubaghs, 1953, p. 683). This plate is thus used to orient young specimens of many hypocrinids (codiacrinids) and allagecrinids, in which an anal plate or opening is not developed until the onset of maturity.

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SYSTEMATIC PALEONTOLOGY

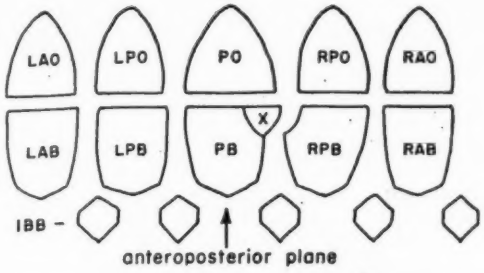
Genus: PENTECECRINUS Koenig and Niewoehner, n. gen.

(Greek: *pente*, five; *-ekes*, pointed; *krinon*, lily)

Type species: *Pentececrinus parvus* Koenig and Niewoehner, n. sp.

Diagnosis.—Dicyclic inadunate crinoid; armless; without RR. Calyx composed of 3 circlets of plates (IBB, BB, OO) plus anal plate. Anal plate within basal circlet in notch between PB and RPB beneath right side of PO. Five OO situated interradially, directly above corresponding BB; each oral furnished with a single vertical protuberance; PO with tallest protuberance, other protuberances progressively shorter counterclockwise from PO, ending with slight elevation on LPO. Five subequal BB occupy most of lower half of calyx. Five subequal IBB, radial in position, make up one-tenth of calyx height. Basal part of IBB circlet marked by circular cicatrix (Fig. 1).

Remarks.—There appear to be two lines of phylogenetic development which evolve from *Pentececrinus*. Both lines of descent are marked by a leftward (clockwise) lateral shifting of the anal in respect to the posterior basal and a similar type of movement of the oral plates in respect to the basal plates. In one lineage the orals, by extension of the left side of the posterior oral, shift leftward toward a radial position while the posterior oral and anal retain their positions relative to each other and to the posterior basal; the anal beneath the right side of the posterior oral and the latter above the posterior basal. This condition persists until Permian time, when the posterior oral and anal also migrate to the left: *Pentececrinus*

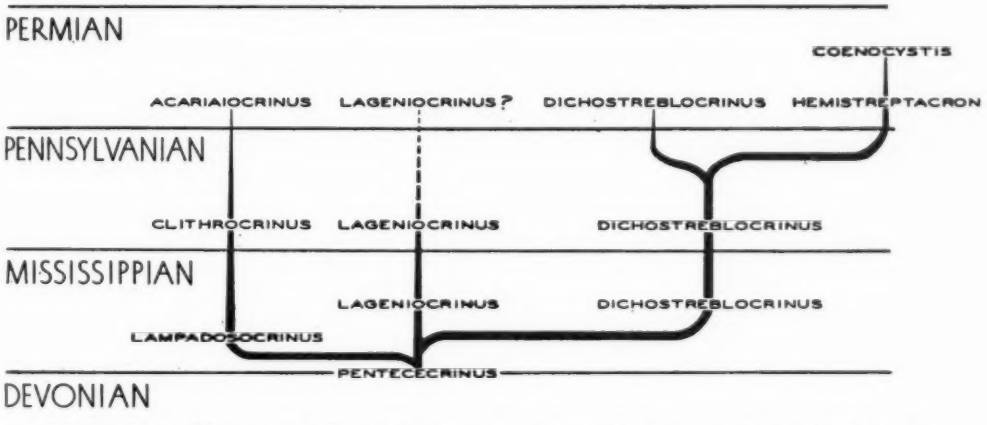


TEXT-FIG. *1*—Analysis of calyx structure of *Pentececrinus parvus* Koenig & Niewoehner, n. sp.

(Devonian-Mississippian), *Lampadosocrinus* (Lower Mississippian), *Clithrocrinus* (Lower Pennsylvanian), and *Acariaiocrinus* (Permian) (Fig. 2). In the other lineage, the orals shift uniformly with respect to the basals, and the anal migrates from the right to the left side of the posterior basal: *Pentececrinus* (Devonian-Mississippian), *Lageniocrinus* (Lower Carboniferous, Lower Pennsylvanian, and Permian ?), *Dichostreblocrinus* (Lower Mississippian, Lower Pennsylvanian, and Permian), *Hemistreptacron* (Permian), and *Coenocystis* (Permian) (Fig. 2). Accompanying modifications of the calyx structure in both phyletic groups are: 1) reduction of the number of infrabasals from five to three plates to an ankylosed disk, and 2) gigantism, in that the general increase in size from an adult specimen of *Pentececrinus* (height, 0.6 mm.) to an adult specimen of *Acariaiocrinus* (average height, 5 mm.) is about 8.5 times and to an adult specimen of *Coenocystis* (estimated height, 8 mm.), about 13.5 times. By analogy, if we applied these increases to future human development, the descendants of a 6-foot man of today would eventually become 50 to 80 feet tall. Similar phyletic size increase is displayed by the Permian genus *Calceolispongia* (Teichert, 1949, p. 42).

Lampadosocrinus Strimple and Koenig, 1956 is the closest morphologic and chronologic relative of *Pentececrinus*—the senior author has collected numerous specimens of *Lampadosocrinus* from the Compton formation (Kinderhookian) of southwest Missouri. *L. obtusus* from the Osagean, Lake Valley formation, of New Mexico (Strimple and Koenig, 1956, p. 1245) possesses five infrabasals, five basals, and five orals. However, the holotype lacks an anal plate or opening (thought to be the result of immaturity), does not possess pronounced protuberances on its orals (although they are distinctly tumid), and has its oral plates slightly and uniformly off-set from corresponding basals.

Mature specimens of *Lampadosocrinus minutus* (Peck), 1936 from the Osagean, Fern Glen formation, of Missouri (Peck, 1936, p. 289) and from the Osagean, St. Joe formation, of Oklahoma (Strimple and Koenig, 1956, p. 1245), however, possess a distinct anal notch between the upper right shoulder of the posterior basal and the upper left shoulder of the right posterior basal beneath the right side of the posterior oral. This corresponds to the anal position of



TEXT-FIG. *2*—Diagram of inferred phylogeny of nonbrachiate, nonradial-bearing crinoids.

Pentececrinus. In *L. minutus* the position of the anterior orals and left posterior oral are displaced leftward (clockwise) toward a radial position, while the posterior and right posterior orals remain above their corresponding basals. Apparently, the displacement of the anterior orals and left posterior oral is caused by the extension of the left side of the posterior oral beyond the suture between the left posterior and posterior basals. This places the left posterior oral almost in a radial position. The midsection of each oral is distinctly tumid or, as in younger specimens, developed into a short spinelike projection. It is believed (Strimple and Koenig, 1956, p. 1245) that immature specimens of this species exhibit a more uniform arrangement of the orals and basals, with the orals being more or less uniformly displaced as in *L. obtusus*.

Clithrocrinus (Kirk) 1937 (*Clistocrinus* Kirk, 1937) from the Lower Pennsylvanian (Pottsville ?) of Alaska displays a similar condition of oral displacement (Kirk, 1937, p. 105). However, in this genus, the extension of the left side of the posterior oral is much greater than the leftward extension of the corresponding plate in *Lampadosocrinus*. Thus, the midline of the posterior oral lies directly above the suture between the left posterior and posterior basals. Two other interesting developments are, 1) the position of the anal opening has shifted slightly to the left, in respect to the anal position of related genera already discussed, and 2) the right posterior basal is abnormally wide with respect to the other basal plates and with respect to the same plate in dorsal cups of comparative genera.

This lateral migration of the anal and posterior oral in specimens of the phyletic group represented by *Pentececrinus*, *Lampadosocrinus*, and *Clithrocrinus* culminates in the Permian genus *Acariaiocrinus* Wanner, 1924 of Timor (Wanner, 1924, p. 165; 1929, p. 74) and of Russia (Yakovlev, 1927, p. 186). In this genus, the anal opening is situated on the midline of the posterior basal and is bounded above by the lower right corner of the posterior oral and the lower left corner of the right posterior oral. Thus, the posterior oral is fully radial in position, and the width of the right posterior basal is not any greater than the width of the other basals.

In 1937 (p. 110) when Kirk described *Clithrocrinus*, he was well aware of its relationship to *Acariaiocrinus* because he states that: "Structurally we see in *Clistocrinus* [*Clithrocrinus*] an intermediate evolutionary stage between the Mississippian *Lageniocrinus* and the Permo-Carboniferous (Russia) and Permian (Timor) *Acariaiocrinus* (*Streptostomocrinus*." He also recognized the fact that in these two younger genera "the orals shifted to the left relative to the plates of the dorsal cup" and that "the lateral opening [anal] is larger and has migrated somewhat to the left" in *Clithrocrinus* and "still further to the left" in *Acariaiocrinus*.

In the other lineage, a very close relationship is recognized between *Pentececrinus* and *Lageniocrinus*. But an essential difference exists in that *Lageniocrinus* has only three plates in its infrabasal circlet instead of five. Until Kirk in 1940 redescribed de Koninck's type specimen (*L. seminulum*), the structure of *Lageniocrinus* has been misinterpreted because of the failure to recognize the presence of an anal opening in the dorsal cup. This opening, as figured by Kirk (1940, p. 134, figs. 7 and 8), lies beneath the right side of the posterior oral in a notch between the posterior and the right posterior basals. Kirk (1940, p. 132) also determined that *Sycocrinus jacksoni* Austin and Austin, 1842, from England, is also a *Lageniocrinus*, but in this species there is some question as to the presence of an anal. *L. seminulum* comes from the Viséan of Belgium, and although some doubt existed about the stratigraphic position of *L. jacksoni*, Wright (1952, p. 133) after careful consideration determined that it also is Viséan in age instead of Tournaisian as supposed by Kirk (1940, p. 135). J. M. Weller (1930, p. 32), following Wanner's interpretation of the genus (*L. timorensis*, Wanner, 1920, p. 23) from the Permian of Timor, described the species *L. cassidus* from the Pennsylvanian, Lower Desmoinesian of Indiana. Both species are described as lacking an anal opening, but in other respects they closely resemble de Koninck's type. The absence of an anal may be explained by the fact that in both cases analysis was based on immature specimens. Kirk (1940, p. 137) points out that *L. timorensis* may be "referable to *Embryocrinus*" as a young individual.

Dichostreblocrinus J. M. Weller, 1930, is represented by specimens from the Mississippian, Osagean, of New Mexico (Strimple and Koenig, 1956, p. 1243), the Pennsylvanian, Lower Desmoinesian, of Indiana (Weller, 1930, p. 37), and the Permian of Timor (Marez Oyens, 1940, p. 327). A typical specimen is composed of an ankylosed infrabasal circlet, five basals, and five orals. The anal orifice, as in *Clithrocrinus*, is displayed slightly farther to the left of the corresponding location in *Pentececrinus*, occupying a notch in the upper right shoulder of the posterior basal. It is bordered on the right by the erect, upper left shoulder of the right posterior basal. The orals of *Dichostreblocrinus* are all uniformly displaced about nine degrees left of an interradial position. These features imply a tendency for lateral, leftward shifting of the anal and oral elements in addition to reduction of the number of plates in the infrabasal circlet.

Further development of this tendency can be seen in the genus *Hemistreptacron* Yakovlev, 1926. The three infrabasals of this genus are often fused into an ankylosed disk, and the displacement of the orals is pronouncedly increased. Specimens of the type species, *H. abrachiatum*, from the Permian of Russia have their orals uniformly displaced about 12 degrees to the left of an interradial position (Yakovlev, 1928, p. 314), and the anal is situated on the midline of the posterior oral just left of the midline of the posterior basal. Some immature specimens of this species reflect the ontogeny of *Lampadosocrinus* by having their orals directly above the basals. Occasionally a young specimen will have its anal situated directly on the midline of the posterior basal (Yakovlev, 1928, p. 313).

Specimens of *H. carinatum* and *H. carinatum* var. *ornatum* from the Permian of Timor (Wanner, 1929, pp. 75 and 78) show a more pronounced displacement of the anal and orals. The anal is much farther left of the midline of the posterior basal than the anal in *H. abrachiatum*, and the orals are displaced about 20 degrees from an interradial position.

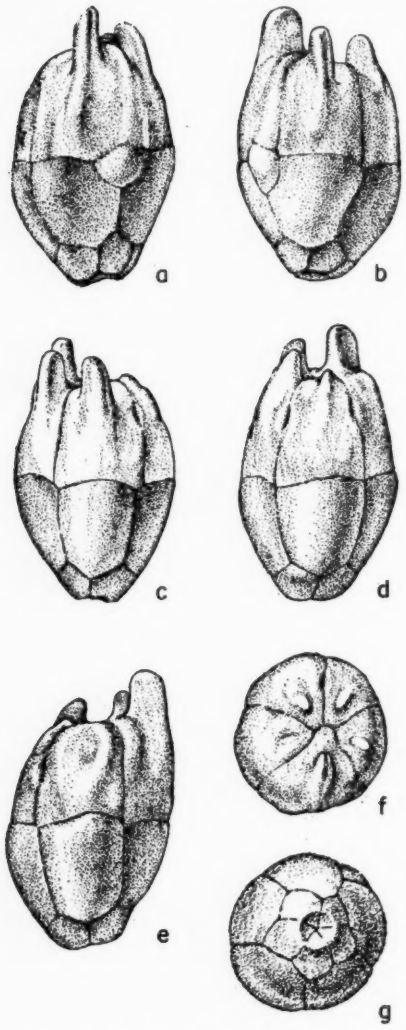
Final development is shown by specimens of *Coenocystis* Girty, 1908 from the Permian of Timor (Wanner, 1924, p. 161; 1929, pp. 79 and 80) and Texas (Girty, 1908, p. 108). The orals of this genus are fully radial in position, and the anal lies at the left extremity of the posterior basal where it occupies a notch between the upper left shoulder of the posterior basal and the upper right shoulder of the left posterior basal. This position is beneath the midpoint of the posterior oral. As Wanner (1929, p. 79) points out, because of this situation, either of the basals bounding the anal can be considered as the posterior basal, but he reasons that because of the close relationship of *Coenocystis* to *Hemistreptacron*, the basal to the right of the anal of *Coenocystis* is the posterior basal.

The genus *Atremacrinus* Wanner, 1929 known only from the type species, *A. calyculus* from the Permian of Timor (Wanner 1929, p. 83), is unique in having, according to Wanner, both the infrabasal and basal circlets ankylosed into a single unit. It also lacks an externally visible anal opening. If this analysis is correct, this genus is comparable with *Tytthocrinus* Weller, 1930 from the Lower Pennsylvanian of Indiana (Weller, 1930, p. 35), and the Lower Mississippian of Missouri (Peck, 1936, p. 291) and New Mexico (Strimple and Koenig, 1956, p. 1241). This latter genus in the adult stage also contains only two circlets of plates, basals and orals, and is considered by Strimple and Koenig (1956, p. 1241) to be fundamentally a dicyclic crinoid, either being pseudomonocyclic or cryptodicyclic according to whether the infrabasls have disappeared through absorption or are merely hidden (Ubaghs, 1953, p. 667). Since the basal circlet of *Tytthocrinus* contains only three plates, it would be possible for these to fuse to form an ankylosed unit, because as evidenced by the infrabasal development of other crinoids, fusion follows after the number of plates in this circlet have been reduced to three.

PENTECECRINUS PARVUS Koenig and Niewoehner, n. sp.
Text-figs. 1 and 3a-g

Description.—Calyx very small, goblet-shaped, composed of three circlets of plates (IBB, BB, OO) and an anal plate; height, not including hypertrophic extensions of OO, 0.59 mm., width, 0.45 mm.; ratio of width to height, 1.31.

Infrabasal circlet small, occupies less than one-tenth of calyx height, composed of five



TEXT-FIG. 3—*Pentececrinus parvus* Koenig & Niewoehner, n. sp., type specimen, ×50; University of Missouri Paleontological Collections E-30–1. Views: *a*, posterior; *b*, right posterior; *c*, right anterior; *d*, left anterior; *e*, left posterior; *f*, ventral; *g*, dorsal.

subequal plates; joins BB without sutural stricture at junction; circular cicatrix at base 0.10 mm. in diameter.

Basal circlet large, occupies about one-half of calyx height, consists of five subequal plates; continues expansion of infrabasal circlet to junction with OO where the configuration of cross section is circular. Plates quadrate and slightly convex, slightly depressed laterally at sutural junctions. Height of circlet, 0.27 mm. Width of RAB, 0.21 mm., other BB, 0.24 mm. PB and RPB appear to be slightly wider distally than the other BB because of slight distortion caused by insertion of anal plate in a deep notch between their mutally opposed upper shoulders.

Anal plate large, triangularly shaped, height, 0.12 mm., width, 0.13 mm.; lies within basal circlet; one-half of plate rests on upper right shoulder of PB and the other one-half on upper left shoulder of RPB.

Oral circlet large, occupies remaining half of calyx height, composed of five subequal plates; height, 0.25 mm. Each oral bears a pronounced, pylon-shaped, vertical protrusion or extension. The largest and tallest extension is situated on the PO which is slightly wider and differently shaped than the other OO and so placed that it prevents the inner extremities of the LPO and RPO from coming in contact. The process on the PO rises 0.135 mm. above the oral surface. Processes on succeeding OO, counterclockwise from PO, are progressively shorter and smaller, forming a steplike series ending with a slight bulge on the mid-upper surface of the LPO.

Remarks.—There is nothing to indicate that the oral processes served a functional purpose for the living organism. The posterior oral apparently lacks a hydropore. There is no indication of its presence in, on, or near the vertical process.

The suture between the posterior oral and right posterior oral is indistinct, but its position is marked by a low, narrow ridge which extends outward and down from the upper surface of the oral dome. As it proceeds down the side of the dome, it widens and flattens, finally merging with the top of the anal plate. It is assumed that this feature marks the position of an internal anal tube which extended upward from the anal plate and was covered over by the posterior oral when the orals were in a closed position in the living crinoid. A similar type of ridge was noted and illustrated in a homeotype of *Lampadosocrinus minutus* (Peck) (Strimple and Koenig, 1956, Text-figs. 4–19) but was not mentioned in the text of their report because of a lack of precedent in other known crinoids and the possibility of its being a

coincidental occurrence. However, with knowledge gained from this unquestionable feature in *Pentececrinus* and with the recognition of the close relationship of the two genera, it is concluded that the ridge on the posterior oral of *Lampadosocrinus* is morphologically valid.

Each of the interoral sutures bounding the left anterior oral possesses a small navel-like depression two-thirds the distance up the side of the oral dome. These depressions are slightly elongated along the sutures, and their interior rounded edges have the appearance of being worn. It is inferred that the depressions resulted from the gentle wearing action of the extended tentacles of the living crinoid when its orals were open or partly open. Similar depressions are not visible on the other interoral sutures.

Despite the fact that there is no visible evidence of radials in the type specimen, the position of the orals in relation to the basals is such that radial plates could be readily introduced into the calyx structure. Thus, it could be argued that this specimen is immature and that future discoveries may disclose mature radial-bearing forms. This is possible, but the following must be taken into account: 1) Although a thousand or more microcrinoid specimens have been extracted from the Louisiana formation by several different persons, the specimen described is the only one of its kind found to date. If the specimen is immature, larger mature specimens should have been reported by now. 2) Studies of growth series of *Allagecrinus*, *Kallimorphocrinus*, *Dichostreblocrinus*, and *Lampadosocrinus* show that the anal plate appears in the calyx structure of these crinoids after the onset of maturity, a condition recognized when the specimens approach maximum size (Weller, 1930, p. 38; Peck, 1935, p. 769; Strimple and Koenig, 1956, p. 1245). 3) The size progression of the oral processes of *Pentececrinus* may be used for recognition of growth stages if it is assumed that the processes make their appearance successively on each oral plate during the life span of the crinoid, beginning with the posterior oral and ending with the left posterior oral. On this premise, the described specimen may be considered as almost fully mature.

The conclusion is that the type specimen is almost fully matured, and if it is a radial-bearing crinoid it should show at least the beginnings of a radial plate somewhere in the calyx structure. Such a plate has not been observed.

Occurrence.—Lower three feet of the Louisiana formation at a location overlooking the Mississippi River, just northwest of Clarksville, Pike County, Missouri, in the SW ¼ sec. 9, T. 53 N., R. 1 E.

Repository.—University of Missouri Paleontological Collections, No. E-30-1.

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JOURNAL OF PALEONTOLOGY, V. 33, NO. 3, P. 471–473, 1 TEXT-FIG., MAY 1959

DEVONIAN STARFISH FROM PIKE COUNTY, PENNSYLVANIA[1]

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ABSTRACT—*Hudsonaster wardi*, sp. nov., an asteroid, is described from the Ludlowville member of the Mahantango formation near Milford, Pennsylvania. This genus has hitherto been known only from the Ordovician.

The starfish exhibits such "primitive" characteristics as few, heavy, non-stellate plates around the disc, and has no accessory ossicles in the arms or disc.

However, this starfish possesses such "advanced" characteristics as having the superomarginal plates almost completely overlap the inferomarginal plates from the apical side. This feature was predicted by Schuchert to be found in post-Ordovician members of the family Hudsonasteridae.

The associated abundant fauna is widespread over the area, and a warm marine environment is suggested. "Storm rollers" indicate that the shallow water was occasionally agitated by strong waves.

SYSTEMATIC DESCRIPTION

Class ASTEROIDEA
Order PHANEROZONIDA Spencer
Suborder PUSTULOSA Spencer
Family HUDSONASTERIDAE Schuchert
Genus HUDSONASTER Stürtz
HUDSONASTER WARDI, n. sp.
Text-Fig. 1

Description.—This is a small starfish with an arm-radius of 4.5 mm. and a disc-radius of 2 mm. The arms are short and taper rapidly; they are composed of three rows of relatively large, pustulose plates. The central row, the radials, are the largest, and the outer rows, the superomarginals, are only slightly smaller except at the proximal area where they are slightly larger. No spines are evident.

Near the axillary angle, the inferomarginal plates can be seen below and alternating with the superomarginal plates.

The disc is bounded by five proximal radials and five interradials. Within the disc is a prominent centrodorsal plate and five smaller plates, arranged in a petaloid manner around the centrodorsal plate and within the radial-interradial ring. The disc is slightly concave in the figured specimen and is probably due to *post-mortem* collapse.

The adapical surface is unknown, and the apical surface is preserved as a mold.

[1] Presented at the Geological Society of America, Southeastern Section, Morgantown, W. Va., May, 1957.

Location and age.—Geographically, the starfish came from a quarry on "The Knob," a spur of land on the Delaware River near Milford, Pennsylvania. It is located on the Milford, Pennsylvania-New York-New Jersey quadrangle, edition of May, 1915, at approximately lat. 41°18′30″ N. and long. 74°48′0″.

Stratigraphically, the age of the rocks in the quarry are Middle Devonian. The following fossils were collected along with the starfish and firmly establish the age:

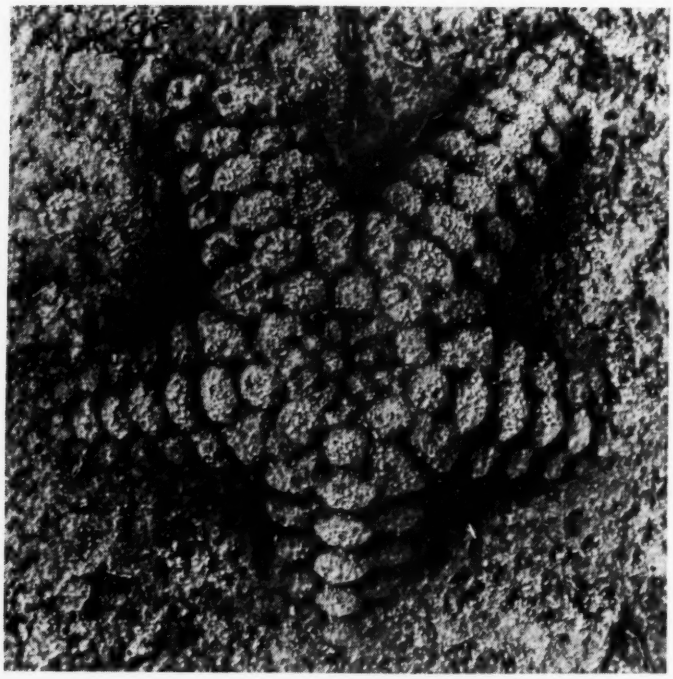
Linguella paliformis (Hall)
Spirifer tullius Hall
Stropheodonta spp.
Cornellites chemungensis (Conrad)
Dipleura dekayi Green
Greenops boothi (Green)

Furthermore, small nodules, called "storm rollers" are common in the quarry. This fauna and the storm rollers are reported by Willard (1939) in his discussion of the Devonian of Pennsylvania.

Material.—One well-preserved mold of the apical surface is available only. It was found in the talus on the floor of the quarry and its precise position within the section is not certain. Several man-hours of collecting revealed no more.

The specimen is deposited in the U.S.N.M., no. 133438.

Remarks.—Genus *Hudsonaster* has been previously known only from the Ordovician. This find marks a considerable extension of the biozone, and destroys a previously con-



TEXT-FIG. 1—*Hudsonaster wardi*, holotype. Ludlowville member of Mahantango formation, Pike County, Pa. ×14; cast of apical side; U.S.N.M. no. 133438.

sidered good guide genus to the Ordovician.

Hudsonaster wardi resembles *H. matutinus* (Hall) except that *H. matutinus* has smaller superomarginals than the basal (proximal) radials, and the form and orientation of these plates on *H. matutinus* are quite different from those of *H. wardi*. Furthermore, all the plates of *H. wardi* are pustulose; those of *H. matutinus* are not.

Hudsonaster wardi resembles *H. incomptus* (Meek) except that the latter has stellate basal superomarginals and only ten radial plates in the arm. *H. wardi* has at least eleven radials in the arms and has non-stellate basal superomarginals.

Various other species of *Hudsonaster* differ greatly from *H. wardi* and there would be little chance of confusion should they be compared. Only the oral surface is known on many of the other species also and comparison is not possible at this time.

The name *Hudsonaster wardi* is given to remember the willingness of Mr. James Ward, of Lancaster, Pennsylvania, to donate his specimen to the world literature once the unusual nature of the find was determined.

EVOLUTIONARY SIGNIFICANCE

The recognition of this form not only extends the range of this genus, but gives considerable information about the evolution of the asteroids.

"Primitive" characteristics.—Schuchert (1915, p. 54) states that geologically later species of *Hudsonaster* have stellate plates in the ring of ten which form the bulk of the disc. This trend does not hold true, apparently, because *H. wardi*, the youngest species now known, has non-stellate plates forming this ring.

Spencer (1914, p. 63) notes that early forms of *Hudsonaster* have larger superomarginals than the later forms. *H. wardi*, however, the latest form geologically, has much larger superomarginals than would be expected if this trend were to hold true.

Another primitive feature possessed by

Hudsonaster wardi is its lack of accessory ossicles in the disc or arms. Most later asteroids have added these plates.

Advanced characteristics.—Schuchert (1915, p. 45) states:

> In *Hudsonaster* the prominent superomarginal plates of the dorsal apical side are placed decidedly inside of the inferomarginals, though the former clearly overlap the latter. This primitive condition is retained in many Paleozoic genera, and apparently not before the Devonic do these columns of ossicles come to lie wholly upon one another, and then they together margin the animals.

Here is a condition noted in some genera and species known in 1915 which is anticipated as a trend and which is borne out in a new *Hudsonaster* of Devonian age which was not known at the time of the prediction.

PETROGRAPHY

The starfish was found in brown, thin-bedded, subangular siltstone which contains scattered carbonaceous material. A slight tendency toward layering of the light and dark materials is evident, although it is not persistent enough to be considered banding.

PALEOECOLOGY

The beds are unquestionably marine, and the abundant and varied fauna suggest warm, shallow water. The silty bottom supported many crawling forms, such as trilobites, starfish, and unlisted pelecypods. There is no sign of extreme agitation in the fossil-bearing beds as the bulk of the specimens are found intact, and the only fragmental materials are crinoid columnals.

The storm roller zone, however, does contain fragments of the fossils and considerable carbonaceous material. A period or periods of agitation is suggested by this occurrence, although it is strange that only one zone occurs.

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QUANTITATIVE TRILOBITE STUDIES III. *PROLIOSTRACUS STRENUELLIFORMIS* POULSEN, 1932

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ABSTRACT—The measurements presented by Poulsen for four species of *Proliostracus* are compared statistically and graphically, and it is concluded that only one species is represented. The name *Proliostracus strenuelliformis* is selected, with the names *P. rosenkrantzi*, *P. liostracoides*, and *P. noe-nygaardi* suppressed as synonyms. The meaning of the regression equations is discussed for each pair of dimensions.

INTRODUCTION

THE four species *Proliostracus strenuelliformis*, *P. liostracoides*, *P. noe-nygaardi*, and *P. rosenkrantzi*, described by Poulsen (1932, p. 49–53) from the Ella Island Formation of Greenland, have been chosen for the first specific analyses in this series for several reasons. First, they illustrate what can be done with data now to be found in published literature. Second, they provide an example of how quantitative analysis of specimens may change taxonomic conclusions. Third, they pose a simple analytic problem because of the comparatively small number of measurements. Fourth, their analysis was a necessary facet of a study of Lower Cambrian ptychoparioid genera to be presented elsewhere.

ACKNOWLEDGMENTS

The author is indebted to Messrs. L. A. Lasnik and David Moles, of Shell Oil Company, Denver, for their help in teaching him the use of the I.B.M. 650 Computer used in analyzing the data and for their assistance in programming the data on these and several other species yet to be discussed. Drafting of the figures was done by Mr. Wayne T. Swinghamer. Permission to publish has been granted by the Shell Oil Company.

DATA AVAILABLE AND METHODS OF ANALYSIS

Poulsen presented, as part of his description of the four species, measurements of six dimensions of each cranidium. These measurements, in the terminology and symbolism suggested by the present author (Shaw, 1957), are:

Total cranidial length (A_1)
Occipital glabellar length (B_1)
Palpebral cranidial width (J)
Posterior cranidial width (J_1)
Transverse occipital length (K)
Anterior glabellar width (K_5)

For the convenience of the reader, Poulsen's data are reproduced in Table 1.

Inasmuch as both Poulsen and Lochman (1947, p. 68) had affirmed the validity of the four species it was assumed at the beginning of the study that the species were distinct. In order to express these differences quantitatively, all possible combinations of

TABLE 1.—MEASUREMENTS OF *Proliostracus* IN MILLIMETERS
From Poulsen (1932). Italicized measurements estimated

Specimen	A_1	B_1	J	J_1	K	K_5
P. strenuelliformis I	2.0	1.5	2.5	3.2	1.0	0.7
P. strenuelliformis II	4.3	3.0	5.3	6.5	2.2	1.7
P. strenuelliformis III	4.4	3.0	5.3	*6.5*	2.2	1.7
P. rosenkrantzi	3.3	2.5	4.3	5.0	1.8	1.3
P. liostracoides	2.3	1.7	2.7	3.2	1.2	0.8
P. noe-nygaardi	5.5	3.8	*7.0*	8.3	3.0	2.0

the six measurements given by Poulsen were plotted graphically. These graphs are presented as Figures 1–15, and the discussion of their significance is the purpose of this paper. After the graphs had been plotted and it became clear that the arrays are rectilinear, rectilinear regression formulae ($Y=a+bX$) were computed for all 15 combinations. In addition, reduced major axes were computed after the method described by Imbrie (1956). The equations and other pertinent statistics are presented in Tables 2 and 3.

It should be noted that the differences between treatment of the data on Poulsen's species by the linear regression or the reduced major axis techniques is very small. This is because the data are unusually rectilinear in their distribution. As any array of points departs from true linearity (where the coefficient of correlation (r) = 1.000) the reduced major axis becomes less and less accurate as an expression of the relation of any X to any Y. A detailed examination of the adequacy of the R.M.A. will be presented at a later date. For this study either set of formulae could be used without essential differences in the results, but in the discussion that follows only the linear regression equations are considered.

MEANING OF THE LINEAR REGRESSION FORMULA

One of the problems that must inevitably be faced in the use of linear regression stems from the fact that the formula does not generally evoke any mental image. Thus, while such a statement as, "The glabella is approximately two-thirds as long as the cranidium" gives a picture to most readers, an approximately equivalent formula:

$$B_1=0.001+0.670\ A_1$$

does not normally call up the same picture. However, an understanding of such equations must come if we are to express our knowledge of morphology, ontogeny, and (it is to be hoped) taxonomy with precision. To that end, a short discussion of the meaning of the regression (or R.M.A.) formula is given as a preface to the description of the species.

The rectilinear regression formula $\hat{Y}=a+bX$ comprises four parts. X, the dimension that is known, and $\hat{Y}$, the dimension that is to be computed, are obvious and need no discussion. Reduced to its simplest elements, all descriptive work is a series of statements about a series of X's—either their absolute values or their values relative to other dimensions (Y's).

In much current trilobite literature the ratio

$$\frac{Y}{X}$$

has been used as a descriptive tool. The author (1956, p. 1212–1214) has discussed ratios and pointed out that they are only adequately descriptive for growth series when $a=0$, so that

$$Y=a+bX$$

becomes

$$Y=bX$$

$$\frac{Y}{X}=b$$

An examination of the graphs presented in Figures 1–15 and in other articles dealing with trilobites shows that a line of regression passing through the origin is exceptional. Theoretically, too, it should be unusual for an array to pass through the origin for that would mean specimens with zero dimensions, an obvious absurdity, or specimens in which X and Y are in fixed proportion at birth and in which the relative size of X and Y does not change ontogenetically. This second condition may, but rarely does, obtain.

Let us return to b, the coefficient of regression. As we noted above, b equals Y/X in lines passing through the origin. It is the measure of the relative size of the dimension Y at a given dimension of X. In the general case, where the line does not pass through the origin b does not equal Y/X but instead, by manipulation:

$$Y=a+bX$$

$$Y-a=bX$$

$$b=\frac{Y-a}{X}$$

Hence, we see that a is the amount that must be algebraically subtracted from Y to get the true value of b. In a figurative sense, a is the "lead" or "lag" which Y has at the

TABLE 2.—EQUATIONS AND OTHER STATISTICS FOR *Proliostracus*

Linear Regression				Reduced Major Axis		
$\hat{Y}=bX+a$	S	σ_b	r	$\hat{Y}=bX+a$	S_d	σ_b'
$\hat{B}_1=0.644A_1+0.243$	0.079	0.026	.9967	$\hat{B}_1=0.646A_1+0.236$	0.131	0.033
$\hat{A}_1=1.542B_1-0.351$	0.123	0.063		$\hat{A}_1=1.548B_1-0.365$		
$\hat{J}=1.273A_1-0.107$	0.169	0.056	.9961	$\hat{J}=1.278A_1-0.125$	0.192	0.036
$\hat{A}_1=0.780J+0.112$	0.132	0.034		$\hat{A}_1=0.783J+0.098$		
$\hat{J}_1=1.504A_1-0.016$	0.173	0.057	.9971	$\hat{J}_1=1.509A_1-0.032$	0.186	0.031
$\hat{A}_1=0.661J_1+0.032$	0.115	0.025		$\hat{A}_1=0.663J_1+0.021$		
$\hat{K}=0.542A_1-0.070$	0.090	0.030	.9940	$\hat{K}=0.546A_1-0.082$	0.168	0.045
$\hat{A}_1=1.822K+0.171$	0.164	0.100		$\hat{A}_1=1.833K+0.150$		
$\hat{K}_5=0.389A_1-0.046$	0.075	0.025	.9919	$\hat{K}_5=0.392A_1-0.057$	0.185	0.062
$\hat{A}_1=2.531K_5+0.174$	0.192	0.162		$\hat{A}_1=2.552K+0.146$		
$\hat{J}=1.975B_1-0.585$	0.090	0.046	.9989	$\hat{J}=1.977B_1-0.590$	0.091	0.019
$\hat{B}_1=0.505J+0.301$	0.046	0.012		$\hat{B}_1=0.506J+0.299$		
$\hat{J}_1=2.324B_1-0.554$	0.218	0.112	.9954	$\hat{J}_1=2.335B_1-0.582$	0.212	0.039
$\hat{B}_1=0.426J_1+0.260$	0.093	0.021		$\hat{B}_1=0.428J_1+0.249$		
$\hat{K}=0.842B_1-0.275$	0.059	0.030	.9974	$\hat{K}=0.844B_1-0.281$	0.072	0.029
$\hat{B}_1=1.181K+0.339$	0.070	0.042		$\hat{B}_1=1.185K+0.333$		
$\hat{K}_5=0.601B_1-0.186$	0.079	0.041	.9909	$\hat{K}_5=0.606B_1-0.200$	0.135	0.055
$\hat{B}_1=1.634K_5+0.350$	0.131	0.111		$\hat{B}_1=1.649K_5+0.330$		
$\hat{J}_1=1.178J+0.129$	0.161	0.042	.9975	$\hat{J}_1=1.181J+0.116$	0.189	0.029
$\hat{J}=0.845J_1-0.086$	0.136	0.030		$\hat{J}=0.847J_1-0.098$		
$\hat{K}=0.426J-0.025$	0.053	0.014	.9979	$\hat{K}=0.427J-0.029$	0.121	0.026
$\hat{J}=2.337K+0.076$	0.124	0.076		$\hat{J}=2.342K+0.067$		
$\hat{K}_5=0.303J-0.001$	0.095	0.025	.9870	$\hat{K}_5=0.307J-0.019$	0.290	0.066
$\hat{J}_1=3.218K_5+0.119$	0.309	2.262		$\hat{J}=3.260K_5+0.061$		
$\hat{K}=0.359J_1-0.055$	0.102	0.022	.9923	$\hat{K}=0.362J_1-0.070$	0.269	0.051
$\hat{J}=2.744K+0.236$	0.282	0.172		$\hat{J}_1=2.766K+0.195$		
$\hat{K}_5=0.257J_1-0.034$	0.084	0.018	.9898	$\hat{K}_5=0.260J_1-0.049$	0.300	0.058
$\hat{J}_1=3.811K_5+0.242$	0.323	0.274		$\hat{J}_1=3.850K_5+0.188$		
$\hat{K}_5=0.704K+0.030$	0.119	0.072	.9796	$\hat{K}_5=0.718K+0.002$	0.202	0.082
$\hat{K}=1.364K_5+0.036$	0.165	0.140		$K=1.392K_5-0.002$		

TABLE 3.—CONSTANT STATISTICS FOR ALL COMPARISONS
(For explanation of symbols see Shaw, 1956, 1957)

	A_1	B_1	J	J_1	K	K_5
$\bar{x}$	3.633	2.583	4.517	5.450	1.900	1.367
σ	1.230	0.795	1.571	1.855	0.671	0.482
σ'	1.815	0.758	2.962	4.131	0.540	0.279
$\Sigma(x-\bar{x})^2$	9.073	3.788	14.808	20.655	2.700	1.393

P for all r's <0.01
N for all pairs $=6$

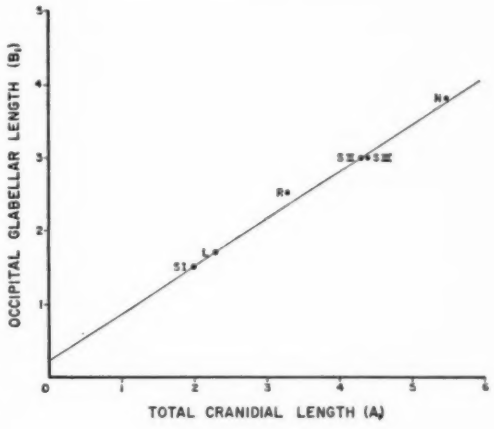
σ computed with N
σ' computed with $N-1$

theoretical instant when X equals zero. Since X cannot trully equal zero in a trilobite and still have existence, this meaning of a is abstract. It should also be clear from the last equation that as the absolute value of a increases the accuracy of the ratio

$$b=\frac{Y}{X}$$

as a descriptive tool decreases, because Y alone is a progressively poorer estimate of $Y-a$.

In résumé, the linear regression or reduced major axis formula expresses the relative size of the two dimensions (b) and the initial "lead" or "lag" in the size of the Y dimension.



TEXT-FIG. 1

DISCUSSION OF REGRESSIONS

A brief examination of Figures 1–15 will make it clear that the four species described by Poulsen are based on various growth stages of a single species. It is impossible for the author to view such remarkably rectilinear arrays and still find any basis for specific differentiation. This conclusion is embodied in the formal synonymy presented at the close of this article.

Total cranidial length (A_1) *vs. occipital glabellar length* (B_1).—In general terms, the glabella, including the occipital ring is about two-thirds as long as the cranidium (Fig. 1). This is more precisely expressed by the value

$$b=0.644$$

but at the same time the value

$$a=0.243$$

shows that the occipital glabellar length (B_1) started out in early stages of growth considerably greater than the value of b alone would indicate. Thus, the complete regression

$$\hat{B}_1=0.644\ A_1+0.243$$

accurately expresses that fact, common in trilobite ontogeny, that the glabella is proportionally longer in smaller heads than in larger. Substituting values of 1–6 mm. for A_1 we find the following computed values of $\hat{B}_1$

A_1	$\hat{B}_1$	$\hat{B}_1/A_1$
1 mm.	0.887	.887
2	1.531	.7655
3	2.175	.725
4	2.819	.705
5	3.463	.693
6	4.107	.6845

From these calculated values two things become clear: (1) The ratio of occipital glabellar length to total cranidial length constantly changes with growth so that no single ratio can adequately describe the proportions of the two parts, except at a specific growth stage. Nor can an average ratio and its standard deviation do so. (2) No simple ratio between B_1 and A_1 approaches the true proportion between the parts ($b=0.644$) until a full grown size is attained. Even in a cranidium 6 mm. long, which is longer than any noted by Poulsen, the ratio $\hat{B}_1/A_1$ has only dropped to 0.6845 or 0.0405 larger than b.

The relation between these two measurements expressed with the occipital glabellar length (B_1) as X is

$$\hat{A}_1=1.542\ B_1-0.351$$

Similar substitution in this formula produces the following ratios:

B_1	$\hat{A}_1$	$\hat{A}_1/B_1$
1	1.191	1.191
2	2.733	1.3665
3	4.275	1.425
4	5.817	1.454

These figures show the same inadequacies of the ratio as a descriptive expression.

A Note on Limitations

In both of the small tables given above values of the X dimension have been given as low as 1 mm. This appears to be safe because Specimen I of *Proliostracus strenuelliformis* is nearly this small. But consider what happens if, in the first formula:

$$\hat{B}_1=0.644\ A_1+0.243$$

we substitute the value

$$A_1=0.5\text{ mm.}$$

The answer then becomes

$$\hat{B}_1=0.322+0.243=0.565$$

implying that

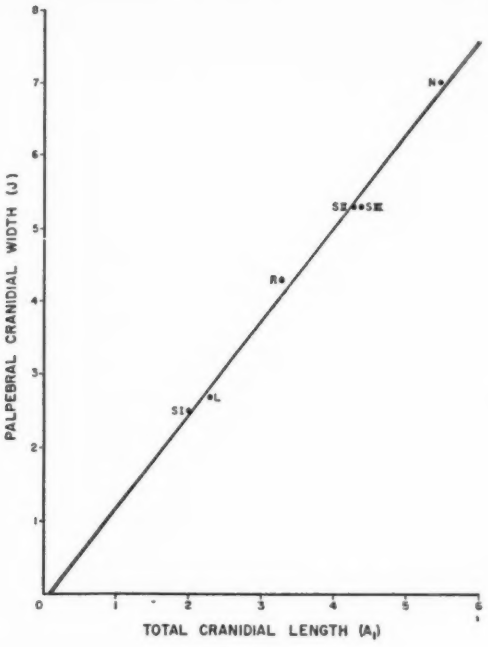
$$\hat{B}_1>A_1.$$

Experience shows that in ptychoparioids of the general type of *Proliostracus* this is not in fact the case. The explanation is a simple one, but it points out a danger inherent in the unthinking application of these formulae: In dealing with very small trilobites the growth is apparently not rectilinear. Palmer's (1958) study of early stages of *Crassifimbra walcotti* has demonstrated from specimens what is derived logically from a consideration of the formula.

Is it not incorrect, then, to use rectilinear regression to express the ontogeny of trilobites? Apparently not in samples that do not include protaspids. Some of the sets of data now under study have been fitted to various exponential curves to determine how much improvement in fit these more elaborate equations provide, and the results show only a slight reduction in the variance. It appears that the post-protaspid portion of the trilobite growth curve is so nearly straight that it can be expressed by the rectilinear regression or reduced major axis formulae without danger.

The limitation of both rectilinear methods, then, is that they will not correctly express growth in the protaspid stages. Hence, it is unsafe to extrapolate downward into the smaller sizes on the basis of regressions calculated from post-protaspid specimens. This limitation does not appear to apply to upward extrapolation, because here the curve is becoming more nearly rectilinear as size increases. Data are now at hand which may shed light on the precise points (biologic and mathematic) beyond which extrapolation from rectilinear equations should not be carried, but for the present it seems safe to say that calculations should not be forced beyond the middle of the range of the meraspid stages. In practice this will not be an undue burden because of the rarity of large collections of protaspids and meraspids.

Total cranidial length (A_1) vs. palpebral cranidial width (J) and posterior cranidial width (J_1).—These two comparisons (Figs. 2,3) are so commonly used to express general cranidial proportion (or "shape") that they are most easily considered together. When most writers describe the cranidial shape in such terms as "transverse," "subquadrate," or "elongate" they are usually referring to the proportions of the cranidial length to either the width across the eyes or the width across the posterior limbs. The proportional width of the frontal area seems



TEXT-FIG. *2*

to enter into qualitative description only when that area is narrowed to the point where such adjectives as "subtriangular" are needed.

Generally speaking, a cranidium is said to be "subquadrate" when both the palpebral (J) and posterior (J_1) cranidial width are subequal to the total cranidial length (A_1). A cranidum is "transverse" when these two width dimensions are greater than total cranidial length (A_1). In an "elongate" cranidium

$$A_1 > J$$

and usually

$$A_1 > J_1$$

In these terms the cranidium discussed here would be transverse, for

$$\hat{J} = 1.273\ A_1 - 0.107$$
$$\hat{J}_1 = 1.504\ A_1 - 0.016.$$

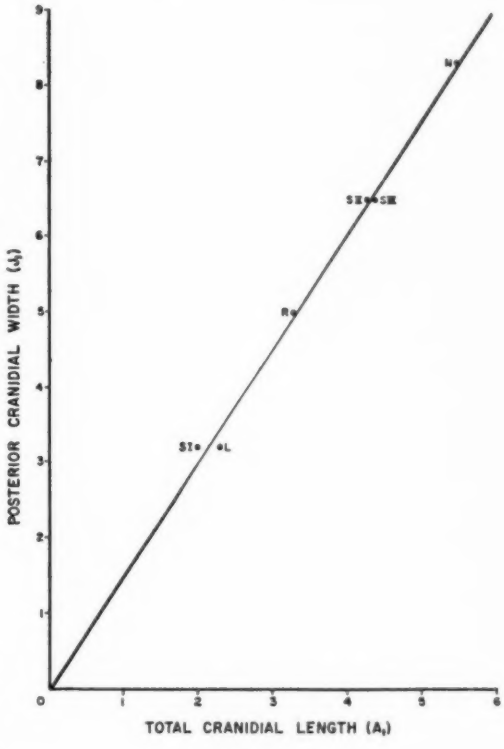
(Also see additional discussion of posterior limb shape below in the comparison of J and J_1.) The small value of *a*, especially in the second formula, indicate that *b* is a fairly good estimate of $\hat{Y}/X$ at most growth stages unlike the formulae relating A_1 and P_1, where *a* represented a large fraction of the value of *b*. Calculated values for the formulae are given in the table below for comparison with those given above.

X	$\hat{J}$	$\hat{J}/A_1$	$\hat{J}_1$	$\hat{J}_1/A$
1	1.166	1.166	1.488	1.488
2	2.439	1.2195	2.992	1.496
3	3.712	1.237	4.496	1.499
4	4.985	1.246	6.000	1.5000
5	6.258	1.252	7.504	1.5008
6	7.531	1.255	9.008	1.5013

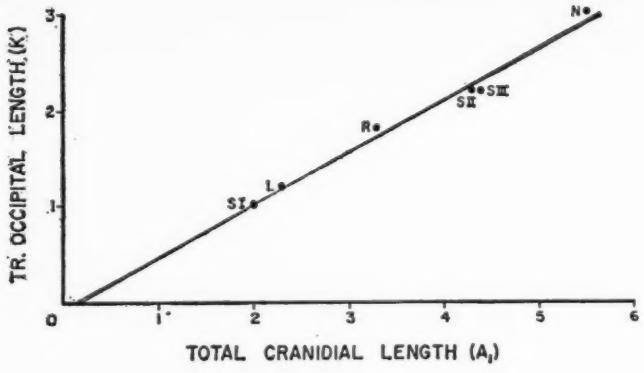
Note how closely the ratio $\hat{J}_1/A_1$ approaches the value

$$b = 1.504$$

This is an illustration of the point made above that as *a* approaches zero, the ratio $\hat{Y}/X$ becomes more accurate as a descriptive tool. But note that the best correspondence occurs only in the larger size groups where the value of *a* is least effective.



TEXT-FIG. *3*



TEXT-FIG. 4

The corresponding formulae with X and Y reversed are:

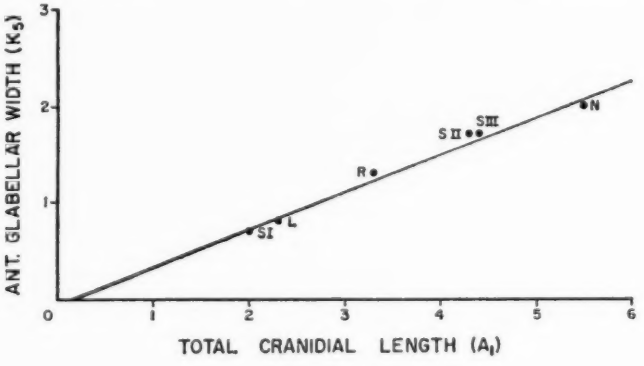
$$\hat{A}_1 = 0.780\ J + 0.112$$
$$\hat{A}_1 = 0.661\ J_1 + 0.032$$

These equations express precisely the facts that the total cranidial length (A_1) is 8/10 as great as the palpebral cranidial width (J) and 2/3 as great as the posterior cranidial width (J_1).

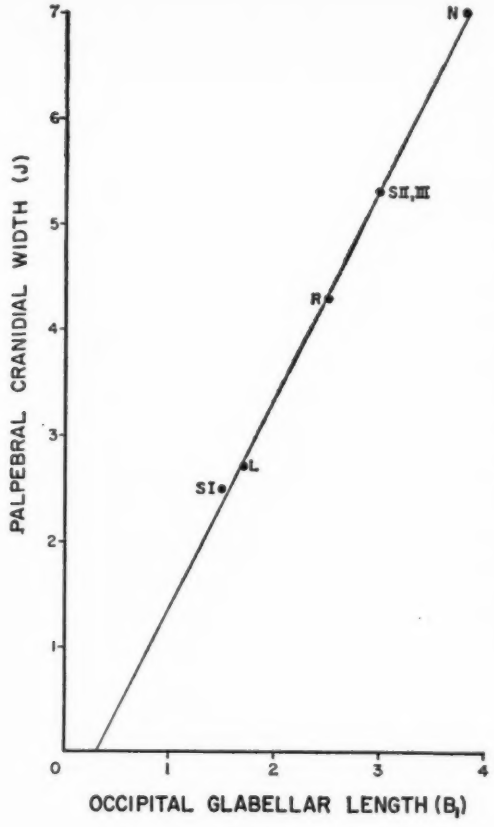
Total cranidial length (A_1) *vs. transverse occipital length* (K).—This correlation (Fig. 4) is not a common one in descriptive work and is included here only to show that Poulsen's measurements for this pair also fall in rectilinear array.

Total cranidial length (A_1) *vs. anterior glabellar width* (K_5).—This combination (Fig. 5) is likewise not a common one. It also shows no evidence of specific separation.

Occipital glabellar length (B_1) *vs. palpebral cranidial width* (J).—Comparison of these two dimensions (Fig. 6) is not commonly made in current descriptive work, but some of the results obtained in other quantitative trilobite studies not yet published suggest that it may be very useful morphologically and informative biologically to use the occipital glabellar length (B_1) as a standard of reference for size in addition to the total cranidial length (A_1). As has long been common knowledge, the growth of the glabella does not follow the same regimen as the length of the cranidium as a whole but instead lags behind it ($\hat{B}_1 = 0.644\ A_1 + 0.243$). For example, in seven of eight studies now completed the position of the eyes is more closely correlated with the length of the glabella (B_1) than with the cranidial or cephalic length (A_1 or A). In addition, there is the practical consideration that in damaged cranidia the length of the glabella is more often determinable than is the cranidial length. It seems quite likely that



TEXT-FIG. 5



TEXT-FIG. 6

as more quantitative studies are carried out the various measures of glabellar length will come to play a more important role than they now do in description.

The formulae for B_1 and J are

$$\hat{J}=1.975\ B_1-0.585$$

$$\hat{B}_1=0.505\ J+0.301.$$

They show an almost exact 2-for-1 increase of J per unit increase in B_1, but the large values of *a* in both equations show that the ratios for these dimensions would not be usable.

In the only comparable species thus far studied quantitatively, *Billingsaspis adamsii*, the formulae are basically different:

$$\hat{J}=1.585\ B_1+1.025$$

$$\hat{B}_1=0.609\ J-0.498$$

This expresses the fact that a shorter glabella is found in *Billingsaspis* than in *Proliostracus*, but that the cranidium is wider, for equal glabellar lengths, in *Proliostracus*. Since most current descriptive procedure tends to view the width of the cranidium as the more normal reference dimension, most students of trilobites would be inclined to say that *Billingsaspis* has a shorter glabella than *Proliostracus* rather than that *Proliostracus* had a wider cranidium. As was pointed out above it is not yet entirely clear that one form of expression is necessarily preferable over the other from a strictly morphologic (or even biologic?) point of view. This is the problem of finding truly comparable variables, as discussed by Miller & Weller (1952).

Occipital glabellar length (B_1) *vs. posterior cranidial width* (J_1).—This comparison (Fig. 7) is not one that is commonly in use, but as mentioned above, it may at times be an advantage to use the glabellar length as a standard measure of "growth," and if this is done the formulae

$$\hat{J}_1=2.324\ B_1-0.544$$

$$\hat{B}_1=0.426\ J_1+0.260$$

will serve as a good description of the position of the points at which the posterior branches of the facial sutures cross the posterior cranidial margin.

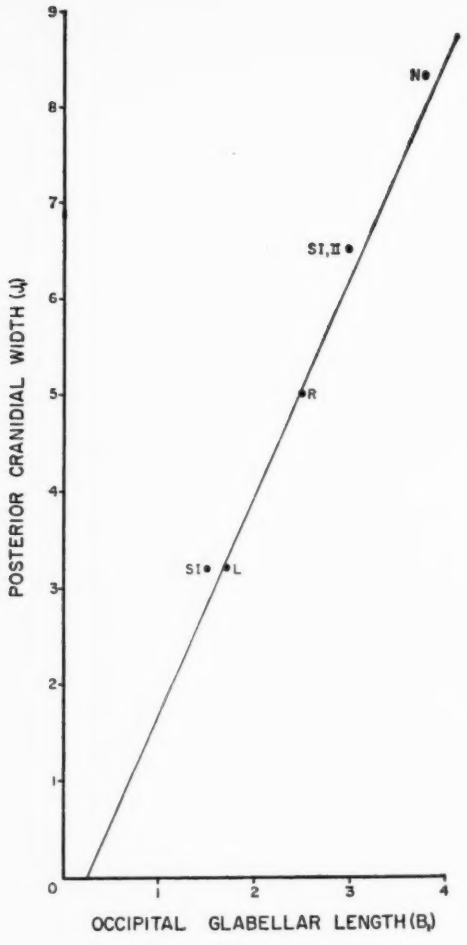
The equations show (by the high values of *a*) that the proportions of these two dimensions change strongly during growth. The glabella becomes proportionately shorter, or the posterior cranidial width becomes proportionately greater in larger cranidia. As in previous comparisons there is no significant deviation from rectilinearity in the proportions of the parts and no significant difference from normal ontogenetic change is apparent among the specimens.

Occipital glabellar length (B_1) *vs. transverse occipital length* (K) *and anterior glabellar width* (K_s).—These two comparisons (Figs. 8,9) are commonly made in descriptive studies, and they may be considered together. The two sets of formulae are:

$$\hat{K}=0.842\ B_1-0.275$$

$$\hat{B}_1=1.181\ K+0.339$$

and

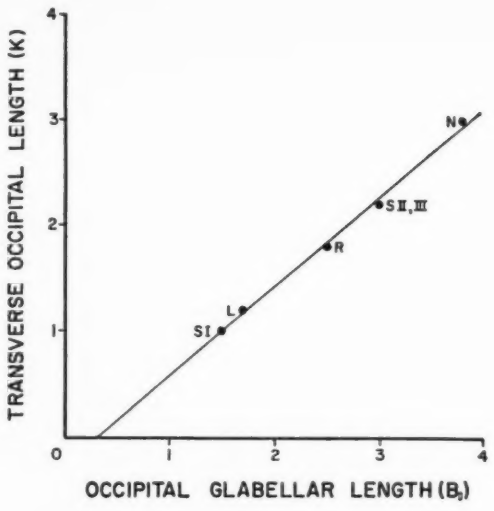


TEXT-FIG. 7

$$\hat{K}_5 = 0.601\ B_1 - 0.186$$
$$\hat{B}_1 = 1.634\ K_5 + 0.350$$

The equations express the fact that at both the anterior and posterior ends the glabella is narrower than its length. Comparison of the values of b in the first and third equations also shows that the glabella tapers forward (*i.e.*, the glabella could not be called parallel-sided or flaring). It would be a simple matter to convert these values trigonometrically into an angle of convergence, but this has not been deemed useful.

The equations also show that K is increasing at a faster rate ($b = 0.842$) than K_5 ($b = 0.601$). Since this is true, it means that by reversing the process we may assume

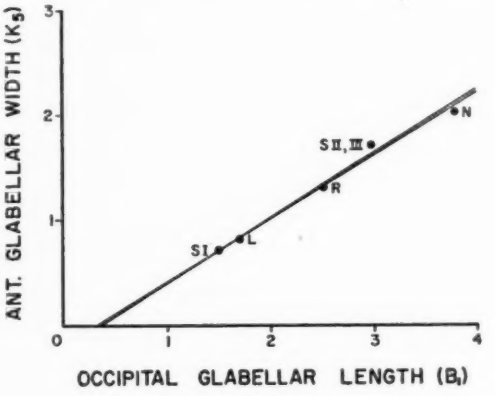


TEXT-FIG. 8

that at some early stage the value of K will have decreased to the point where it equals K_5. This point may be determined by equating the two formulae:

$$0.842\ B_1 - 0.275 = 0.601\ B_1 - 0.186$$
$$B_1 = 0.37 \text{ approximately}$$

This value of B_1 is only a quarter of that of specimen I of *P. strenuelliformis* and is small enough so that the caution against undue downward extrapolation of rectilinear regression probably applies. But in spite of this it is encouraging to note that a study of the equations alone leads to a conclusion concerning glabellar shape that we can regard as almost certainly correct from



TEXT-FIG. 9

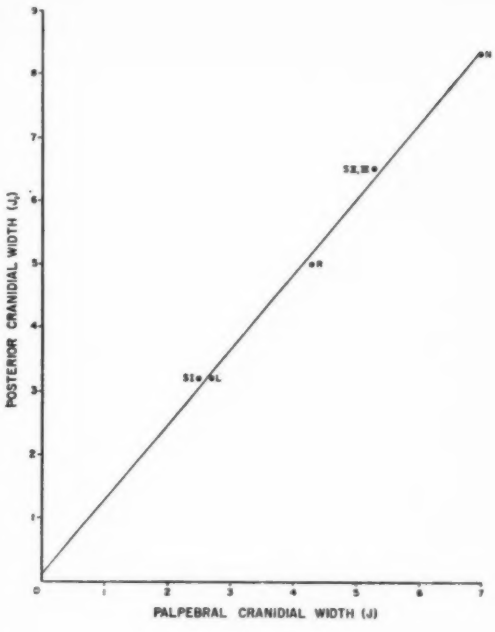
studies of other ptychoparoids of this general form (*i.e.*, that the glabella becomes parallel-sided in young stages although not necessarily at $B_1 = 0.37$ mm.).

In addition, if we wish to press the point—possibly too far—there is a hint that the glabella may have been slightly flared anteriorly in the very smallest stages. This is certainly true of the early stages of the not-too-distantly related species described by Palmer (1958, text-fig. 7; pl. 26, fig. 2,3). A problem that obviously needs investigation is whether ptychoparoids always show growth patterns expressible in equations homologous to those found here. If so, then the early stages of these trilobites would all show anteriorly flared glabella, which in turn might prove to be one of that class of features which d'Arcy Thompson (1952, esp. chap. 5) has shown to be forced on an animal mechanically and, thus, not to be of ontogenetic or phylogenetic (recapitulatory) significance. It appears to the present author that one of the most important of the possible contributions of quantitative study of trilobites is the elucidation of such relations as that shown here, among the occipital glabellar length (B_1), the transverse occipital length (K) and the anterior glabellar width (K_5).

Palpebral cranidial width (J) vs. posterior cranidial width (J_1).—The two regression formulae for this pair of dimensions (Fig. 10)

$$\hat{J}_1 = 1.178\ J + 0.129$$
$$\hat{J} = 0.845\ J_1 - 0.086$$

show that the two widths increase at almost the same rate, although the posterior width is slightly greater at all stages than the palpebral width. Morphologically this means that the eyes are not notably "set in" toward the glabella, as compared to the posterior limbs. Another way to describe the relation is to say that the posterior limbs are not prominent. In species with wide, prominent posterior limbs the value of *b* in the first formula will be higher than it is here (generally 1.5 or above). Thus, this comparison is an effective means of expressing quantitatively the prominence of the posterior limbs. As in the previous instances, there is no separation of the individual specimens other than that attributable to growth.



TEXT-FIG. *10*

Palpebral cranidial width (J) vs. transverse occipital length (K).—This combination of dimensions (Fig. 11) is not commonly used and is included here only for completeness. The equations

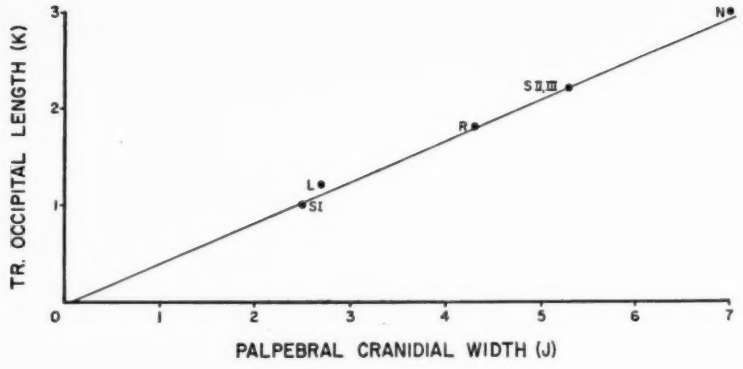
$$\hat{K} = 0.426\ J - 0.025$$
$$J = 2.337\ K + 0.076$$

show by their small values of *a* that the proportions of these two width measurements do not change seriously during growth. There are no specifically significant differences among the specimens.

Palpebral cranidial width (J) vs. anterior glabellar width (K_5).—This comparison (Fig. 12) is not one that is normally made, but it nearly approximates the more common comparison of the palpebral cranidial width (J) with the palpebral glabellar width (K_1). The equations

$$\hat{K}_5 = 0.303\ J - 0.001$$
$$\hat{J} = 3.218\ K_5 + 0.119$$

show that the anterior glabellar width (K_5) is almost exactly equal to the width of the fixed cheeks. Since the value of *a* is nearly zero, this ratio will obtain down to the smallest sized heads.



TEXT-FIG. *11*

Posterior cranidial width (J_1) *vs. transverse occipital length* (K).—This comparison (Fig. 13) is a standard one in current descriptive work although it is usually framed as a comparison of the length (tr.) of the posterior limb (L or L_1) with that of the occipital ring (K). The formulae here are:

$$\hat{K}=0.359\ J_1-0.055$$
$$\hat{J}_1=2.744\ K+0.236$$

They show that the occipital ring occupies almost exactly a third of the posterior cranidial width (J_1) and, therefore, that the posterior limbs and occipital ring have equal lengths (tr.). It would be a simple matter to make the usual comparison by first obtaining the transverse length of the posterior limb (L) by subtraction:

$$L=\tfrac{1}{2}(J_1-K)$$

and then preparing a regression lines for the relations

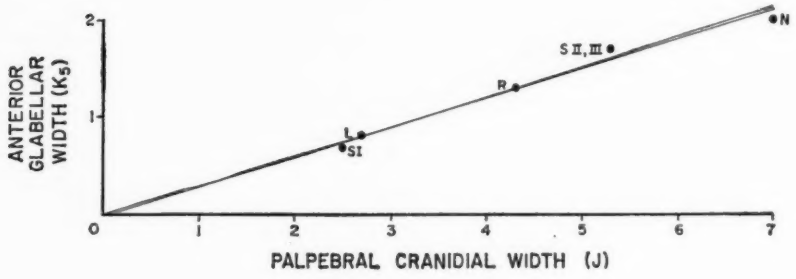
$$\hat{L}=bK+a$$
$$\hat{K}=bL+a$$

but it did not seem necessary to make this calculation since the comparison of the dimensions given by Poulsen show directly proportions of the occipital ring and posterior limbs.

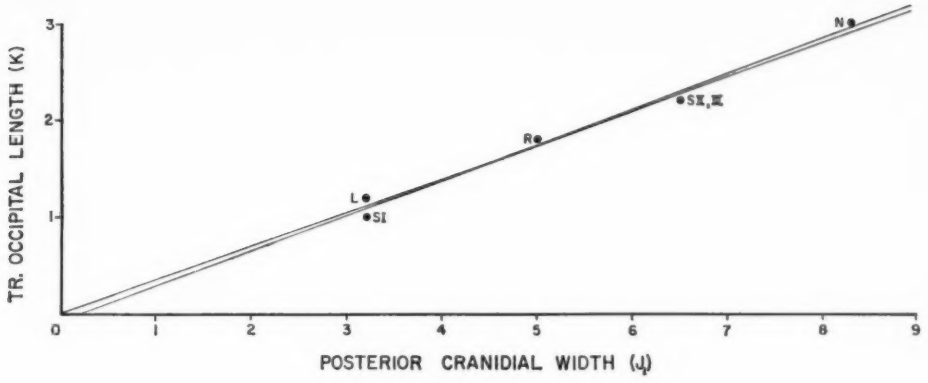
Posterior cranidial width (J_1) *vs. anterior glabellar width* (K_5).—This comparison is rarely, if ever, made in current descriptive work. The graph (Fig. 14) shows that there is more divergence between the lines of regression than in the other comparisons, although the coefficient of correlation ($r=0.9898$) is still highly significant ($P<0.01$). The equations are:

$$\hat{K}_5=0.257\ J_1-0.034$$
$$\hat{J}_1=3.811\ K_5+0.242.$$

The slight discrepancy in the slopes of the two lines is probably due to the fact that these two dimensions are the two most likely to error in measurement. It is often difficult to be sure of the exact point where the posterior limbs end in specimens preserved in limestone, so that slight errors are



TEXT-FIG. *12*



TEXT-FIG. *13*

introduced. Likewise, it is difficult to be sure that exactly equivalent measurements are taken on a tapering glabella from one specimen to the next. Experience with other trilobites has shown that these two dimensions (J_1 and K_5) and the width of the posterior limb (L or L_1) are the most likely to suffer from error of measurement.

Transverse occipital length (K) vs. anterior glabellar width (K_5).—This relation, shown in Figure 15, expresses the degree of taper in the glabella. The equation

$$\hat{K}_5 = 0.704\ K + 0.030$$

shows that there is a slight tapering of the glabella toward the front. The taper does not change remarkably with growth, as shown by the low value for *a*, although the glabella in small cranidia are proportionately less tapered than in adults. The reversed equation

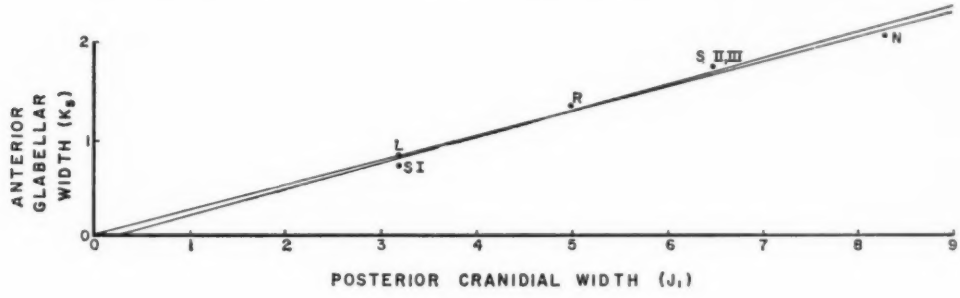
$$\hat{K} = 1.364\ K_5 + 0.036$$

likewise shows an essentially unchanging proportion of the two dimensions, and the graph shows an essentially rectilinear pattern of growth.

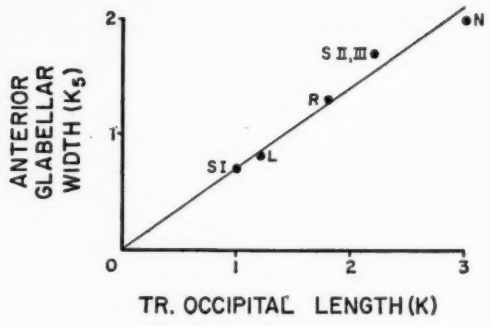
EVALUATION OF DISTINCTIONS MADE BY POULSEN

In discussing the four species, Poulsen (1932, p. 49) stressed the elevation of the glabella above the fixed cheeks. In *P. strenuelliformis* and *P. rosenkrantzi* the elevation is "inconsiderable." In *P. liostracoides* and *P. noe-nygaardi* the elevation is "considerable." A study of the pictures shows that this feature is due to the exfoliation of the latter two, which, therefore, have better-impressed furrows. The remaining features, such as the depth and width of furrows and the curvature of the anterior end of the glabella are either the result of preservation or slight differences between individuals.

Poulsen also cited a wider (sag.) occipital ring in *P. strenuelliformis* than in *P. rosenkrantzi*. Unfortunately, he did not supply



TEXT-FIG. *14*



TEXT-FIG. *15*

measurements so that the difference could be checked, but measurement of the figures shows that *P. rosenkrantzi* is intermediate in this respect between the smallest head of *P. strenuelliformis* (Pl. 14, fig. 6) and the remaining cranidia (Pl. 14, figs. 1, 2, 4), and is also intermediate in size between these two groups. Thus, the distinctions in proportion among the four species are due to ontogenetic change, and the remaining differences appear to be due either to variability among individuals or to the vagaries of preservation.

Inasmuch as there are four names for the species, *Proliostracus strenuelliformis* Poulsen, 1932, is chosen to stand and the remaining three are suppressed. A formal synonymy is given below.

PROLIOSTRACUS STRENUELLIFORMIS
Poulsen, 1932

Proliostracus strenuelliformis POULSEN, 1932, Medd. om Grønland, Bd. 87, no. 6, p. 49–50, pl. 14, fig. 1–6.——, LOCHMAN, 1947, Jour. Paleontology, vol., 21, p. 68.

Proliostracus rosenkrantzi POULSEN, 1932, *op. cit.*, p. 50–51, pl. 14, fig. 7,8.——, LOCHMAN, 1947, *loc. cit.*

Proliostracus liostracoides POULSEN, 1932, *op. cit.*, p. 51–52, pl. 14, fig. 9,10.——, LOCHMAN, 1947, *loc. cit.*

Proliostracus noe-nygaardi POULSEN, 1932, *op. cit.*, p. 52–53, pl. 14, fig. 11,12.——, LOCHMAN, 1947, *loc. cit.*

The original description of the species may be modified as shown below. Alterations are shown by italics; omissions by dots.

Species represented by *15* cranidia.

Cranidium transverse

$$(\hat{J}_1 = 1.504\ A_1 - 0.016),$$

moderately convex, with evenly curved brim. Brim slightly convex, rather wide (*sag.*) in front of the glabella, tapering gradually toward the facial suture, separated from the preglabellar field and the anterior part of the fixed cheeks by a poorly defined marginal furrow. Preglabellar field a little wider (*sag.*) than the *brim*, sloping toward the glabella *and with a low median swelling.*

Glabella of moderate length

$$(\hat{B}_1 = 0.644\ A_1 + 0.243)$$

strongly convex *in exfoliated specimens, moderately convex where the test is preserved,* . . . truncate *or slightly rounded* in front; *tapered* ($K_5 = 0.704\ K + 0.030$), with *three or* four pairs of short . . . glabellar furrows. The anterior pair of glabellar furrows *is* represented by shallow pits *just behind* the anterior corners of the glabella; the following three pairs of glabellar furrows *are* a little longer than the *first* pair, narrowing rapidly toward the dorsal furrow; the sece ond and fourth pairs of . . . furrows *ar*slightly oblique. . . . Occipital furrow . . . wide and shallow, almost uniformly impressed throughout; *furrow shows medial anterior deflection in some exfoliated specimens.* Occipital ring wide (*sag.*), tapering . . . *laterally.*

Furrow around front end of glabella narrow, distinctly marked; posterior part of dorsal furrow *broadens* to form simply the bottom of the wide depression surrounding the glabella. *In exfoliated cranidia, the entire furrow is indistinct.*

Fixed cheeks strongly convex, sloping forward, backward, and toward the glabella; *equal in width* (*tr.*) *to the anterior glabellar width* (K_5)*; slightly narrower than palpebral glabellar width* (K_1). Ocular ridges indistinct, oblique. Palpebral lobes strongly elevated, *lying slightly anterior to the middle of the occipital glabellar length* (B_1). Posterior marginal furrow *always well marked but of variable depth.* Posterior marginal rim narrow, rounded.

Anterior branches of the facial suture almost straight, parallel or converging slightly *anteriorly;* posterior branches . . . almost straight, forming angles of about 45° with the posterior margin of the cranidium. *Posterior limbs not notably wide* ($\hat{J}_1 = 1.178\ J + 0.129$). *Occipital ring occupies one-third of*

the posterior cranidial width ($\hat{K}=0.359\ J_1 -0.055$).

Surface of the cranidium finely granulate; *internal molds minutely pitted.*

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MANUSCRIPT RECEIVED SEPTEMBER 24, 1958

NOMENCLATURAL NOTES

THREE NOTES ON SILURIAN WORM GENERA

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LOCKPORTIA, NEW NAME FOR THE SILURIAN WORM GENUS *DCATYLETHRA* RUEDEMANN, PREOCCUPIED

In 1925 Rudolf Ruedemann (New York State Mus. Bull. no. 265, p. 44, 45, pl. 15, fig. 12) proposed the genus *Dactylethra* for a genus of worms from the Gasport lens of the Middle Silurian Lockport formation of New York, with *Dactylethra conspicua* Ruedemann as the type species. But *Dactylethra* had been proposed by Cuvier in 1829 (Regné Animal, 2nd edit., v. 2, p. 107) for a genus of amphibians. The name *Lockportia* is therefore here proposed for Ruedemann's genus, with *Dactylethra conspicua* Ruedemann as the type species.

RUEDEMANNELLA, NEW NAME FOR THE SILURIAN WORM GENUS *BERTIELLA* RUEDEMANN, PREOCCUPIED

In 1925 Rudolf Ruedemann (New York State Mus. Bull. no. 265, p. 43, 44, 45, pl. 14, figs. 3, 4) proposed the genus *Bertiella* for a worm from the Upper Silurian Bertie waterlime of Buffalo, New York, with *Bertiella obesa* Ruedemann as the type species. But *Bertiella* had been proposed for another genus of worms by Stiles and Hassal in 1902 (Science, n. ser., v. 16, p. 434). The new name, *Ruedemanella*, is therefore here proposed for Ruedemann's genus, with *Ruedemanella obesa* (Ruedemann) as the type species.

NEW GENUS FOR *SERPULITES CURTUS* SALTER, 1848

The serpulid worm from the Middle Silurian Wenlock formation of Abberley, in Worcestershire, England, that was described by J. W. Salter as *Serpulites curtus* in John Phillips' Memoirs of the Geological Survey of Great Britain and the Museum of Practical Geology in London, v. II, pt. I, 1848, p. 333, pl. 30, fig. 1, 2, is not properly referable to the genus *Serpulites*, Murchison, The Silurain System, 1839, p. 700, and does not appear to belong in any other described genus. The new genus, *Sinuocornu*, is therefore here proposed for it. Species of this genus have a short, rather rapidly tapering, sinistrally curved, tube, shaped like the sinuous horn of a cow. The genotype is *Serpulites curtus* Salter 1848, which now becomes *Sinuocornu curtum* (Salter). The three syntype tubes of this species (the only ones known), which are in the collection of the Geological Survey and Museum, in London, are said by Salter to exhibit on their outer surfaces moderately strong and oblique lines of growth.

JOURNAL OF PALEONTOLOGY, V. 33, NO. 3, P. 488-499, 2 TEXT-FIGS., MAY 1959

SYMPOSIUM ON FIFTY YEARS OF PALEONTOLOGY

ADEQUACY OF THE FOSSIL RECORD

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ABSTRACT—During the history of the Paleontological Society there have been many important developments in paleontology. In addition to steady increase in knowledge through new fossil discoveries, increasing attention is being given to ecological and evolutionary processes, and there is growing concern with theory and principles in both the biological and geological aspects of paleontology. There is, however, a neglect of comparative morphology and taxonomy, and there are far too few expert paleontologists to cover the work to be done.

For a qualified few who recognize the challenge, opportunities are almost unlimited in paleontology for significant studies of comparative morphology, systematics, evolution, stratigraphic facies, paleoclimatology, and the general history of life. The utilitarian value of fossils as stratigraphic indicators is, and will always be, an important aspect of paleontology. But, as requirements become ever more exacting, stratigraphic paleontology calls for skilled preparation of fossils and expert knowledge of their biological nature beyond the abilities of the non-specialist.

Intensive stratigraphic studies in all parts of the world, and the development of improved methods of collecting and preparing fossils have revealed a fossil record much richer than was envisioned by the founders of the Paleontological Society. There are now substantial reasons for believing that the available record is still very incompletely known. Much remains to be learned about the processes by which organisms are preserved as fossils.

INTRODUCTION

IT IS a pleasant custom to celebrate the anniversaries of outstanding events and it is appropriate and useful at such times to take note of progress and trends in human affairs. This year, 1958, is the Jubilee anniversary of the founding of the Paleontological Society. It is also the centennial of the first public announcement by Darwin and Wallace of their theory of evolution by natural selection; and it is the bicentennial of the publication of the tenth edition of Linnaeus' *Systema Naturae* from which stems our method of naming animals and plants. This year is also notable as a year of compromise and agreement among paleontologists and neontologists with respect to revisions of the international code of zoological nomenclature. These were all events of great importance in the history of paleontology.

BIRTH OF THE PALEONTOLOGICAL SOCIETY

Fifty years ago, in Baltimore, at a meeting of the Geological Society of America, thirty-four paleontologists convened under the chairmanship of Charles Schuchert to create a new organization of paleontologists out of the existing Society of American Vertebrate Paleontologists. The plan was to broaden the scope of that group to include students of fossil invertebrates and plants. If was thought that it might be mutually rewarding for paleontologists of varied interests to meet together at least once a year to exchange views about the problems of common interest. Thus was born the Paleontological Society, the stated purpose of which was the "promotion of the science of paleontology." The charter members, including many of the greatest figures of American paleontology, wise in the knowledge of their time, were Ami, Arnold, Bagg, Bassler, Beede, Berry, Case, W. B. Clark, J. M. Clarke, Cook, Cumings, Foerste, Gidley, Gilmore, Grabau, Kirk, Knowlton, Loomis, Lull, Matthew, Osborn, Prosser, Raymond, Riggs, Savage, Schuchert, Shimer, Stanton, Ulrich, Walcott, Weller, White, Williams, and Williston.

The program[1] of the first annual meeting of the Society reflected great interest in

[1] Papers by Clarke, Calvin, Bassler, Sinclair, Schuchert, and Knowlton were published in Popular Science Monthly, vol. 76, p. 581-603, 1910. See also, Cleland, 1910.

fundamental problems of paleontology. Two of the papers were devoted specifically to the adequacy of the fossil record and these have suggested the title of my remarks.

In 1908, as now, the study of fossils had many different facets: stratigraphic, morphologic, taxonomic, geographic, ecologic, evolutionary, and so on. For some persons, especially the students of fossil plants and vertebrates, paleontology was an exciting quest providing records of organic evolution, and climates and ways of life long past. For others, mainly invertebrate paleontologists occupied with the practical business of making geologic maps and classifying and correlating strata, paleontology was a kind of philately in which the fossils were the postage stamps and the postmark of their organic origin was ignored. From the very beginnings of our science there have been two schools, those who study fossils in order to understand stratigraphy, and those who study fossils in order to learn about past life. It is unfortunate that these two points of view are sometimes regarded as mutually incompatible because they need not be. They should supplement each other in building a well-balanced science of paleontology. Surely, neither group has a monopoly in the knowledge of fossils and both approaches to paleontology can be rewarding.

In the early days, varied approaches to paleontological problems were judged to be highly beneficial for the science and all aspects of paleontology were well-represented in the Society. In recent years, however, specialization and increasing divergence of objectives have wrought sweeping changes in the Society. The paleobotanists, always few in numbers, now are allied with the Botanical Society. The vertebrate paleontologists have their own society. Many individuals in both groups retain membership in the Paleontological Society. In this way their needs are best served. The activities of a great majority of the members of the Paleontological Society now lean strongly toward the stratigraphic aspects of invertebrate paleontology, physical stratigraphy, and sedimentation.

In a presidential address to the Paleontological Society, G. Arthur Cooper (1958) has given a comprehensive and able summary of recent developments in paleontology. I lend my whole-hearted support to his plea for more paleontology of higher quality. The fossil record is much richer than we formerly supposed and we need to give much more attention to discovery and description of fossils for the purposes of both geological and biological paleontology. This is fundamental.

The opportunities in paleontology are greater and more rewarding than ever before. There is a steady demand by universities, museums, and geological surveys, and petroleum companies for young men who are broadly trained in paleontology and equally expert in studies of fossils and sedimentary rocks. There are many competent stratigraphers but too few of these really understand fossils, and the demand for able paleontologists greatly exceeds the supply. Why is this true?

No doubt this is a reflection of a traditional antipathy of physical scientists for the disorderly nature of biology, an attitude shared, unfortunately, by many stratigraphers with strong preferences for the physical aspects of historical geology. Some of these are charged with teaching paleontology to impressionable university students and thereby transmit and perpetuate their prejudices. In view of the vast contribution to human knowledge that paleontology has made, and continues to make, it is astonishing that this subject receives less recognition among many earth scientists than, say, oceanography, or seismology. Biological geology receives less than enthusiastic endorsement from a majority of physical geologists.

In the physical sciences, particular conditions tend to produce predictable results, within the limits of observational error. For example, the laws of physics and chemistry can be mathematically expressed and their operation can be tested as often as desired. The passage of time does not affect the results. Gravity does not have a history. This appeals to those who feel that nature is inherently systematic and orderly.

In contrast, the situation is infinitely more complex and difficult in the biological sciences because each organism in many ways is unique. Broadly speaking, evolution is irreversible. History does not repeat itself, and a particular type of organism is never

again exactly reproduced after becoming extinct or extensively modified. Every flora and fauna is unlike every other one. The fossil record consists of a succession of evolving forms which vary not only through time but also along each stratigraphic horizon. Many scientists are uncomfortable in the face of such proof of the inherent complexity of organic nature.

Thus, the fossil record and the evolutionary sequences that it illustrates are complex, immeasurably more complex and more difficult of analysis than the record of the rocks. The study of fossils cannot be mechanized through application of labor saving instruments, and it is indeed doubtful that it will ever be possible to study fossils on a truly mass production basis.

Probably these are some of the reasons why stratigraphers now outnumber paleontologists five or six to one in the Palentological Society.

In spite of a chronic shortage of paleontologists, however, there have been remarkable advances in knowledge about fossils in the past fifty years. These include not only the gradual accumulation of new facts through continuous collecting, but they also include revolutionary changes in our methods and attitudes toward fossils. Indications of these changes are found in the mounting flood of great philosophical works, textbooks, and handbooks on fossils that are appearing with increasing frequency. Among these, the *Treatise on Marine Ecology and Paleoecology* and the *Treatise on Invertebrate Paleontology*, both conceived by the membership of this Society, provide impressive testimony of exciting new developments. They clearly show that paleontology is today broader and more vigorous than it was fifty years ago, even though the ratio between productive paleontologists and physical geologists unquestionably has dropped.

Stratigraphic paleontology enjoyed an impetus after the sudden growth of commercial micropaleontology in the early 20's. But the truly revolutionary developments of the past three decades are 1) improvements in techniques of collecting, preparing and describing fossils, 2) recognition of the special importance of populations in taxonomy and evolution, 3) increased attention to the ecological aspects of fossil communities as the key to the meaning of stratigraphic facies, 4) the application of statistical methods in the analyses of all sorts of paleontological problems, and 5) the geochemical studies of fossils. These subjects will, doubtless, be treated in the papers that follow.

Comment is in order here on the recent application of electronic IBM computers in the solution of paleontologic problems. This is, I believe, more than just another statistical technique. Studies of animal morphology by Olson and Miller, and biofacies analysis by John Imbrie, involve statistical analyses of scores of variables. Problems of excessive complexity now can be attacked quickly and efficiently. In the near future, we may have at our disposal the means for more or less routine quantitative solutions of all sorts of paleontological problems involving complex interrelationships of many variables.

WHAT IS THE FOSSIL RECORD?

An important gain in paleontology during the past fifty years has been a gradual increase in appreciation of the positive merits of the fossil record. A century ago, Charles Darwin was preoccupied with the deficiencies in the record, and his two "geological" chapters in the *Origin of Species* reveal a remarkable insight into the problems of stratigraphic paleontology.

In reality, there are two aspects of the fossil record, and it is worth-while to distinguish clearly between them. One is the published, more or less adequately known, record. The other is the undiscovered, but potentially knowable, record. In discussing the nature of the fossil record, few writers have clearly distinguished between the two.

The known record may be regarded as a sample from which we periodically draw inferences, not only about past life but also about the potentially knowable fossil record. The known record increases gradually and our interpretations evolve with new discoveries, but the potentialities of the record do not change. In the remarks that follow, "fossil record" will be understood as the total record unless otherwise qualified.

THE TEST OF RELIABILITY

Fifty years ago, some of the participants in the first scientific sessions of our Society

took a much more optimistic view of the merits of the fossil record than did Darwin. Nevertheless, there is still a lively debate going on with respect to the validity of many general conclusions and inferences from fossils about past life. Doubtless, it may be a long time before we are prepared to make a final evaluation about the adequacy of the record for certain general conclusions. There is general agreement, however, that many striking patterns of fossil distributions have been confirmed independently hundreds of times. Reproducibility of general conclusions in paleontology, as in other sciences, is the best test of reliability. The abrupt appearance of the Cambrian fauna; the rise and decline of the ammonoids, primitive mammals, and trilobites; the explosive spread of the angiosperms; the world migrations of land mammals during the Tertiary; and mass extinctions near the close of Permian, Cretaceous, and Pleistocene times—these and hundreds of other generalizations about the fossil record—are based on a great body of observational evidence. They have been accepted for so long that we regard them as established truths of geologic history.

Not all well-documented paleontological evidence permits unequivocal conclusions, however. For example, modern studies of paleomagnetism in sedimentary rocks have suggested to some investigators great migrations of the magnetic, and possibly the geographic, poles throughout geologic time. Extensive studies of relative growth rates of fossil corals have led Ting Ying Ma likewise to the conclusion that the earth's poles have migrated (Ting Ying Ma, 1957, and earlier papers).

On the other hand, the distribution of land plants after the middle Paleozoic indicates latitudinal zonation in climatic belts approximately parallel to the present equator (Chaney, 1940; Edwards, 1955). Latitudinal zonation is also well-marked among many groups of marine invertebrates; for example, the Cretaceous rudistids and whole faunas of the Permian and Tertiary periods (Stehli, 1957; Durham, 1958).

Well-documented knowledge about distribution of fossils in time and space is cumulative. The extension of known ranges by means of new discoveries does not upset or invalidate earlier conclusions, as is sometimes claimed, but simply requires modification of prior conclusions based on less complete data. For example, the unexpected discovery of living coelacanths and monoplacophorans, supposed to be long extinct, does not affect interpretations of the early history of these animals.

RICHNESS OF THE FOSSIL RECORD

It has long been accepted that the fossil record is not a random sample of past life. For the most part, the record consists mainly of skeletal parts of organisms that lived within, or near, sedimentary basins. Even among these organisms there is only a very poor fossil representation of soft-bodied forms. The organisms of upland areas and deserts are rarely found preserved as fossils. It is often stressed that, on the average, the chances of preservation of individual organisms as fossils are very small, indeed. But it should be kept in mind that the total number of individuals that ever lived, of even the most limited species, is always very great. In spite of low probabilities of preservation, fossils are really not uncommon. It is well-known that the individuals of many fossil species are fantastically abundant in the rocks. Even those fossils considered to be very rare must be represented by thousands or millions of individuals yet to be discovered.

During the past few years we have been compelled to revise our ideas about the overall richness of the fossil record. J. T. Gregory (1955) has shown recently that the numbers of known kinds of fossil vertebrates tend to be roughly proportional to the numbers of collecting sites. While this is certainly not so often true of fossil plants and invertebrates, there can be no doubt that we have hardly yet a good idea of the ultimate richness of the record. Strata considered to be only sparsely fossiliferous, as judged from superficial inspection, actually may contain an abundance of fossils. The degree to which this is true is shown clearly by methods of mass collecting fossils, wherein a volume of sediment or rock is dug by hand, shovel, or power machinery, washed, and sieved for fossils. This method has long been used for microscopic fossils such as spores and Foraminifera, but it also is used effectively now

for collecting larger invertebrates and bones and teeth of small vertebrates. The number of fossils thus obtained usually is greater per unit volume than the number that accumulates over a unit area of rock, and fossils collected in matrix commonly are of better quality than those that have been long exposed to the weather.

Small fossils are incredibly numerous in many strata where they are major components of the rocks. Leidy once estimated a quarter of a million Foraminifera in an ounce of marine sediment. A cubic inch of diatomaceous earth contains as many as fifteen million diatoms per cubic inch and there are many cubic miles of nearly pure diatomite along the Pacific Coast of the United States, alone. Robert Broom, the South African paleontologist, estimated that there are eight hundred thousand million skeletons of vertebrate animals in the Karroo formation. While such estimates, of course, are not highly accurate, they stress the vast difference between the known paleontological sample and the astronomic numbers of fossils remaining in the rocks.

THE NUMBERS OF FOSSIL SPECIES

Many persons have attempted to estimate the total number of fossil species recorded in the literature. Nearly fifty years ago, Schuchert (1910) estimated that there were one hundred thousand fossil species known. A recent tabulation by Muller and Campbell (1954) does not increase the earlier estimate. They find that ninety-two thousand species of fossil animals are known, and I suppose that the record of fossil plants would bring the total to around one hundred thousand.

Teichert (1956) has tried to calculate the total number of "readily preservable" animals and plants that ever lived. He has taken as a premise the view that calcareous, siliceous, or woody skeletons make up most of the fossil record and he omits consideration of soft-bodied organisms and insects, as quantitatively unimportant in the fossil record. In this, I think that he errs because very many of these are known as fossils and, surely, many more will be discovered. Although they probably are not so abundant as individuals, they may eventually exceed other kinds of fossils in variety.

According to Teichert, the numbers of species now living that would be most susceptible to preservation as fossils are:

Invertebrates	170,000
Vertebrates	49,000
Vascular plants	350,000
Total "Preservable species"	569,000

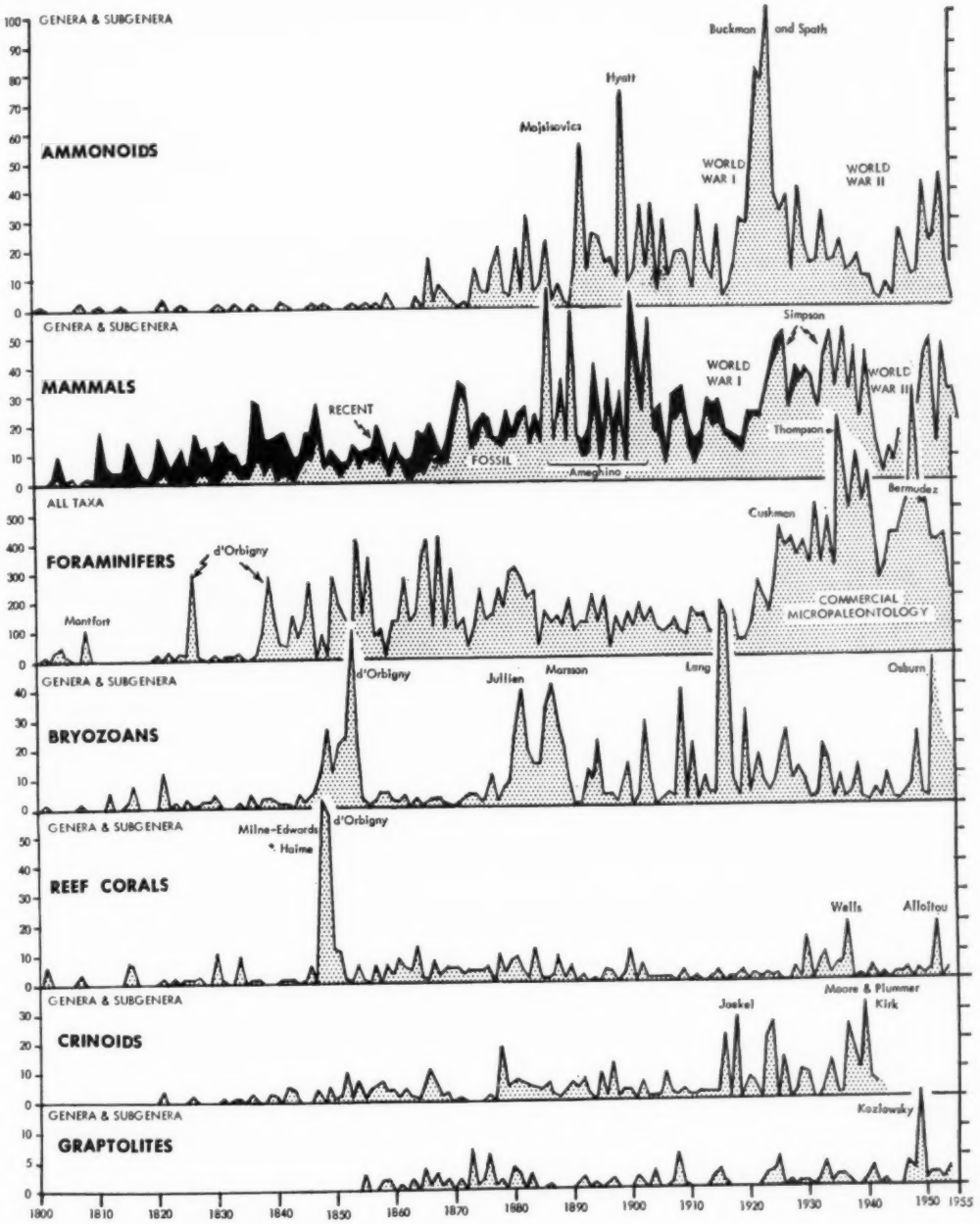
Taking twelve million years as the average length of a geological epoch, therefore the top limit for average longevity of fossil species, he concludes that the number of species of animals and plants preserved in the rocks may reach a total of ten million. I think that the estimate may be too small.

These speculations are useful in stressing the fact that the fossil record is, indeed, poorly known, and they indicate something of the magnitude of the task and opportunities ahead for paleontologists. The known record may represent not more than one percent of the potentially knowable record if Teichert's figures are of the right order. Yet, the known record reveals much of value about past life and serves as the basis for a very respectable stratigraphic system. In any case, it seems absurd to conclude that the heyday of taxonomic paleontology is over. Our problem is not similar to that of mineralogy in which the total number of species probably never will exceed three or four thousand.

RATES OF DISCOVERY OF NEW FOSSILS

A few fossil groups are becoming comparatively well-known and their taxonomy has become stabilized. This is true, for example, of the ammonites, the graptolites, and the hexacorals (Scleractinia), all of which are favored by field geologists and have been studied for a long time by specialists. New discoveries in these groups have little tendency to upset views about general phylogeny. Is there any indication that these or others are so well-known that most of the preserved kinds have already been discovered?

Publication rates provide a rough measure of discovery rates of new categories (Fig. 1). A long-sustained, or increasing publication rate of new taxa, for example, may be an indication that the supply of new



TEXT-FIG. *1*—Fluctuating publication rates in several important groups of fossils. Data from *Treatise on Invertebrate Paleontology*, G. G. Simpson, R. C. Moore, Angelina Messina, and others.

fossils is not near depletion. Minor fluctuations in publication rates are caused by the sporadic publication of monographs and by the different taxonomic philosophies of authors; and larger fluctuations are caused by war, depression, and other human vicissitudes. Long-term trends in publication are certainly significant in terms of the development of knowledge about fossil groups.

Figure 1 indicates that discovery rates in Foraminifera and fossil mammals are accelerating as the search is intensified. Excepting insects, there is no group of organisms under such extensive study as are the Foraminifera and now they may be the best known of any fossil group. According to Miss Angelina Messina (personal communication), twenty-four thousand four hundred and fifty-four species and varieties and one thousand five hundred and twenty-two genera and subgenera are listed in the Catalogue of Foraminifera through the year 1957. In contrast, the rate of publication of new genera of recent mammals gradually has dropped nearly to zero. It may be confidently inferred that nearly all of the living mammals have been discovered (Fig. 1).

The record of the ammonoids is not as clear. There is a suggestion that the rate of discovery of new ammonoids actually is declining, but it is too early to be sure of this. The recent passing of both Spath and Arkell, our leading experts in this group, certainly will cause a marked slump in ammonite studies during the next few years. The other groups of figure 1 show very low and erratic discovery rates that probably are a reflection of the fact that very few persons have worked on these groups. Surely, there is no indication in any of these data that the supply of basically new fossils is about exhausted.

The Scleractinia, or reef corals, are well-constructed for preservation as fossils, and they have been covered in comprehensive summaries by Vaughan, Wells, and others. They may be regarded as a group in which the fossil record is exceptionally well-known. Throughout the West Indian region there are innumerable elevated fossil reefs dating from Pleistocene interglacial stages. These contain a well-preserved coral fauna essentially like that still living in the region. According to Wells (1956), the Pleistocene ice ages did not cause significant extinction among the corals. On the other hand, one-third of the living hermatypic coral genera of the West Indies are not yet known in the Pleistocene rocks of the region (John W. Wells, personal communication), and the Pleistocene faunas are, at least, as well-known as are those of the Tertiary. Undoubtedly, further and more intensive collecting in the Pleistocene reefs gradually will bring to light most of the recent genera and species.

PROBABILITIES OF DISCOVERY

Influenced by the low probabilities of preservation of organisms as fossils, we have a tendency to regard well-preserved fossils as rare objects. This attitude is sure to be strengthened by hasty search or unskilled laboratory preparation. Rocks that actually are replete with well-preserved fossils are often reported as barren, or sparsely fossiliferous because the fossils do not lie in conspicuous view over the surface, conveniently freed by weathering from the rock matrix.

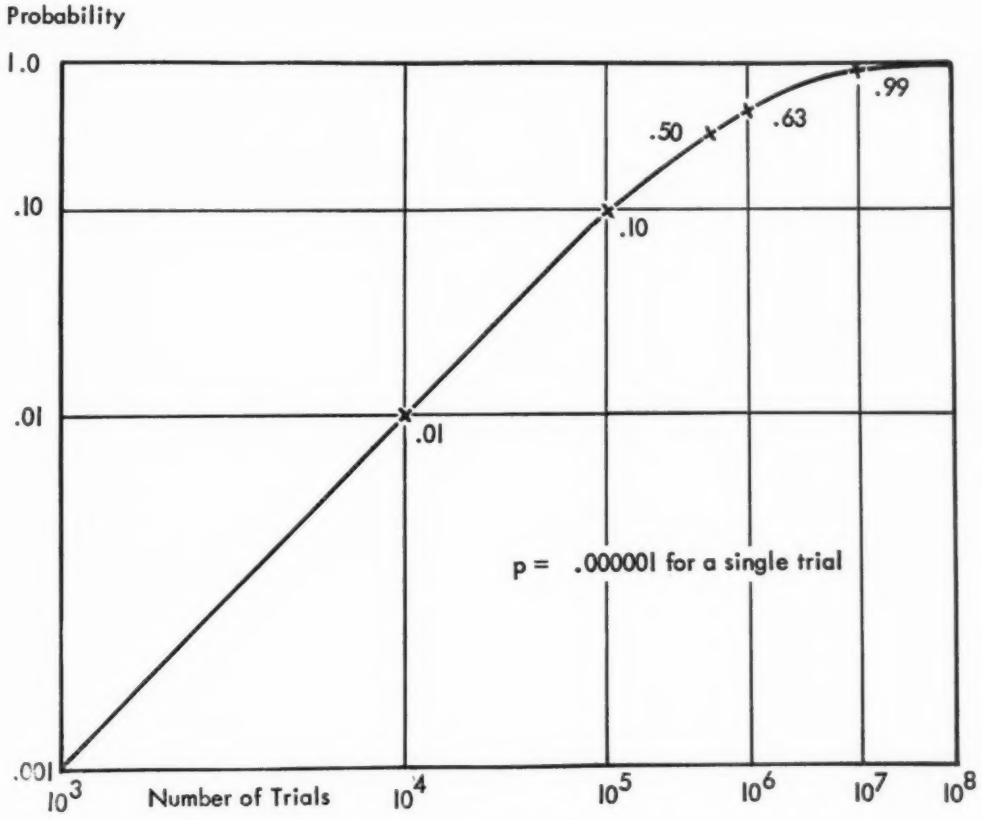
The discovery of fossils is strongly influenced by laws of chance. Consequently, patience and repeated visits to the field usually are rewarded. The preservation of fossils likewise is dependent on the chance coincidence of many factors. There is a fundamental mathematical rule that however improbable an event may be in a single trial that event becomes increasingly probable, or even inevitable, as the trials are multiplied.

The minimum probability that we are concerned with here is that a fortunate combination of circumstances may occur at least once. Among the billions of individual organisms that have made up each species, at least one may be preserved and finally discovered by an appreciative paleontologist. A probability of one to one million for an event to take place in a single trial is clearly highly improbable. If, for the sake of argument, we assume that the chances of preservation of a single organism are of this or any other order of magnitude, the probability may be increased simply by multiplying the number of organisms.

The time element, as well as number of organisms, clearly has a very important

bearing on the chances that a particular species may leave a fossil record. Let us imagine a standing population of thousands or millions of animals that breed only once a year. With an assumed probability of preservation of a really good sample of one in one million (p=.000001) in the first year, the probability of preservation increases to 0.5 in seven hundred thousand years and 0.99 in ten million years (Fig. 2). Thus, a good sample of the species has an excellent chance of becoming part of the record before the species has become extinct. The assumed probability of one in a million is much too low for the very many fossil species that are actually represented abundantly at many localities and horizons and it is too high for species that were not preserved at all.

There are innumerable well-documented records of preservation of tissues of animals and plants in pre-Quaternary rocks (Ladd, 1957). The chitinoid skeletons of eurypterids, graptolites, and chitinozoa, but little changed from the original condition, are not rare in rocks as old as Ordovician. Fossil logs of *Araucaria* with cellular structure and saprophytic fungi perfectly preserved and virtually unmodified by mineralization are abundant in the lower Cretaceous rocks of New Jersey. These were all formerly considered to be extremely rare examples of good preservation of organic substances in fossils, but they are now regarded as fairly common. Obviously, as the search for the potentially available but still unknown record is intensified, the probabilities of discovery greatly increase. Fossils which at first are regarded as rare may accumulate in collections and eventually come to be regarded as common or abundant.



TEXT-FIG. 2—Effects of repeated trials on probability where probability that an event will take place in one trial is one in a million.

QUALITY OF THE FOSSIL RECORD

During the past fifty years, we have steadily become more and more optimistic about the quality, as well as the quantity, of the fossil record. Granted that the processes of preservation are highly selective, there are, nevertheless, innumerable reports of examples of highly improbable preservation. Many of these were unknown fifty years ago. Now they are taken for granted.

Plant tissues decompose very slowly in fine-grained anaerobic bottom-sediments. Unless they are subjected to high temperatures or great pressures they may be preserved almost indefinitely with very little modification, as shown by the New Jersey Cretaceous logs. Animal tissues decompose much more rapidly than plants, but under favorable conditions they may endure for centuries with but little change. For example, large numbers of pre-Christian human cadavers are found in the peat deposits of Denmark and Holland. They are remarkable for excellent preservation of external form and fine details of tissues and organs. Little is known of the physico-chemical environment responsible for this preservation, but experimental work by Franz Hecht at the Senckenberg-am-Meer Institut near Wilhelmshaven (Hecht, 1933) shows in a general way some of the changes that may take place in animal tissues buried in water-soaked sediments. A small shark, buried for two years in water-soaked, anaerobic mud of a tidal flat, was generally well-preserved. The skin and muscles were still firm. After seven years, patches of the skin were recognizable but the carcass had deteriorated badly. Since the surrounding water-soaked sediment was soft and yielding, the body form was mainly destroyed. From his studies, Hecht learned that the protein substances decomposed very rapidly (probably liberating ammonia with resulting elevation of the pH), but the fatty substances decomposed very slowly, gradually passing into the sediment and sealing the organic mass, concretion-like, from surrounding ground waters and oxygen. Under certain conditions, the environment was acid and the shells of associated molluscs were dissolved. In other cases, where sulfate-reducing bacteria were active, the interstitial water became alkaline because of replacement of the strongly acid sulfate by sulfide, and calcareous shells were perfectly preserved. Weeks (1953) has suggested that calcareous concretions that surround fossils may have been formed by precipitation of calcium carbonate in an alkaline environment provided by ammonia from decaying protein substances. This work on fossilization is so suggestive that further studies along these lines might be fruitful.

One of the most remarkable examples of preservation of organic tissues in antiseptic swamp waters is a "fossil graveyard" in Eocene lignite deposits of the Geiseltal in central Germany, made known by Johannes Weigelt and his associates, of Halle University (Weigelt, 1935). Many animals, including groups rarely found as fossils, lower primates, snakes and birds were trapped in several small, scattered bogs where they accumulated and were preserved in anaerobic waters. More than six thousand remains of vertebrate animals and a great number of insects, molluscs, and plants were found in these deposits. The compressed remains of soft tissues of many of these animals showed details of cellular structure and some of the specimens had undergone but little chemical modification. Among the frogs were specimens in which the bones were leached away while the brain and spinal cord were preserved as adipocere Muscle tissue, connective tissue showing microscopic details, and cartilage were found in fishes, frogs, salamanders, lizards, and mammals. Small details of fly larvae and beetles, including muscle tissue, and tracheae were preserved.

Several fossils contained remains of fat cells and pigment cells containing animal pigment. Well-preserved bits of hair, feathers, and scales probably are among the oldest known examples of essentially unmodified preservation of these structures. The stomach contents of beetles, amphibia, fishes, birds, and mammals provided direct evidence about eating habits. Bacteria of two kinds were found in the excrement of crocodiles and another was found on the trachea of a beetle. Fungi were identified on leaves, and the original plant pigments, chlorophyll and coproporphyrin, were found preserved in some of the leaves. From such

ample fossil evidence, Weigelt (*op. cit.*) has reconstructed the Eocene life of the Geisel Valley in considerable detail.

There are innumerable accounts in the literature of fossil bacteria, some of which are of dubious validity. Many, however, are well-documented and are accepted by Zobell (1957). Suggestive associations of fossil bones showing evidence of disease and supposed fossil bacteria formed the basis of a classical monograph on paleopathology by Moodie (1923).

Destruction of organic remains is retarded in impervious rocks which exclude oxygen and prevent the circulation of ground water. Mollusc shells of Cretaceous age are abundant in the Coon Creek clay of Tennessee. The mother-of-pearl shells and even chitinoid ligaments of clam shells are extraordinarily well-preserved for such an old fauna. Caster and Waering (1951) discovered many remarkable articulated skeletons of the eurypterid *Megalograptus* in a clay deposit of Ordovician age. The original chitin is but little altered in these fossils and still retains a scorpionid color pattern. Chitin usually is quickly destroyed by bacterial decomposition under aerobic conditions. The preservation of these eurypterids illustrates the influence of fine-grained matrix on preservation of fossils. The horny substance of graptolites and certain protozoans is also sometimes preserved in fine-grained calcareous rocks.

The most effective preservative of fossils is fine-grained silica which may hermetically seal and protect organic remains from bacteria and ground water for hundreds of millions of years. Probably the most important development in collecting fossil invertebrates in recent years has been the adoption of mass collecting techniques that insure recovery of silicified faunas preserved in delicate detail. Almost nothing is known about the causes of selectivity in silicification of fossils (see Hellmers, 1949), but it appears that there may be two principal modes of silicification. These are not necessarily mutually exclusive and they may simply be successive stages in a single process. In the first case, organic tissues may be impregnated by opaline or cryptocrystalline silica before bacterial decomposition has destroyed essential textures and structures. The process is not yet understood, but it seems to be essentially a kind of embalming of the organic compounds in an impervious matrix of silica. Renault (1901) had circumstantial evidence that the precipitation of silica might be aided by the activities of decay bacteria. Siliceous impregnation evidently proceeds with great rapidity in some cases since remarkably delicate tissues of micro-organisms are often preserved by this means. In the second type of silicification, the original skeletal material is substituted by crystalline quartz; microscopic textures of the original material are not preserved, and the fossil is a pseudomorph of the skeleton. Examples of the two types of preservation will be considered separately.

Remarkable examples of impregnation by silica are filaments and spores of low algae and fungi found in chert of the mid-Huronian Gunflint formation of Ontario, now under study by Barghoorn and Tyler. The oldest known fossils still preserve traces of amino acids after seventeen hundred million years (Barghoorn, 1957; and personal communication).

Until recently, the oldest known land flora was a silicified lower Devonian peat bog found near Rhynie in the Scottish county of Aberdeen. Many species of beautifully preserved primitive vascular plants have been described from this locality together with the remains of many spiders, a mite, and a primitive wingless insect, all impregnated with silica. Silica impregnation is a fairly common mode of preservation of fossil plants, another outstanding example of which are the remarkable Jurassic and Cretaceous Cycadeoids, described by Wieland (1906, 1916).

Perfectly preserved chitinoid tests of early Paleozoic protozoans (Chitinozoa) and graptolites are frequently encountered in chert nodules. A great advance was made when Kozlowski discovered that many of these corneous microscopic fossils could be extracted from the hard matrix by means of hydrofluoric acid which dissolved the silica but did not affect the organic substance of the fossils. Soft-bodied microscopic organisms, including protoplasmic euglenoid protozoans, complete with flagella, have been described in Cretaceous chert in several well-documented reports by Wetzel (1953).

One of the most important discoveries of fossils preserved by siliceous impregnation are extraordinarily well-preserved uncrushed insects and other small arthropods with body hairs, appendages, and some of the internal organs preserved, found in petroliferous, calcareous nodules of Miocene age in the Calico Mountains of California. Allison Palmer (1957) found that many of the insects had been impregnated or coated with a film of silica so that they can be extracted from the calcareous matrix by means of acetic or formic acid with exquisite details intact. This discovery offers a promise that a systematic examination and chemical preparation of calcareous nodules in other formations may lead to a greatly extended knowledge of the history of insects.

Dr. W. D. Pierce, of the Los Angeles County Museum, aided by Mrs. Ruth A. Kirkby, has been systematically collecting and preparing the fossiliferous nodules. Dr. Pierce reports (personal communication) that fifty per cent of the nodules processed have yielded eggs, larvae or adult insects of many orders, with an average of 3.5 insects per nodule. One nodule contained remains of fifty insects.! In addition, there are well-preserved ostracodes, scorpionids, centipedes, mites, fairy shrimp, fish, impressions of feathers, mammal hairs, moss, algae and leaves of higher plants. Twenty-six silicified fish eggs have been found containing various stages of the embryos.

Phosphatic coprolites sometimes contain well-preserved micro-organisms that have been impregnated with silica. For example, Wilmot Bradley (1946) has described well-preserved micro-organisms of several kinds in fossil coprolites of Eocene age from Wyoming. Fossil feces belonging to reptiles and mammals contained a profusion of intestinal saprophytes closely similar to those of living forms. In addition, one of the mammalian coprolites contained large numbers of fresh water algae. The bacteria and algae were impregnated with silica and show microscopic details of structure.

These and innumerable other examples of fossils impregnated with amorphous or microcrystalline silica demonstrate the superiority of this mode of preservation and they suggest that small fossils preserved in this way are common in the fossil record.

It has been known for a long time that certain fossils may be extracted from hard rock matrix without damage by means of acids which either dissolve the matrix without affecting the fossils or dissolve the fossils without affecting the matrix. In the latter case, the resulting cavity may be used as a mold to restore perfectly the external form of the organism or skeleton. Perhaps, because of the relatively high cost of the acids in former days, this method of preparing fossils never was extensively exploited until about thirty years ago. G. Arthur Cooper has developed refined methods of preparing fossils at the U. S. National Museum by means of dilute acids. Many kinds of plants, invertebrates, and vertebrates are being successfully prepared in this way. In certain limestones and dolomites many of the calcareous fossils have been selectively replaced by silica without appreciable modifications of the calcareous matrix. The soluble rock matrix may be carefully dissolved away from the fossils with suitable acids. This method combines the advantages of mass collecting with chemical preparation and fossils preserved in this way as siliceous pseudomorphs are almost certainly more abundant than generally supposed. From thirty to forty tons of Permian limestone collected in the Glass Mountains of Texas, Cooper has extracted an estimated three million invertebrate fossils, the majority of which are exquisitely preserved. The morphology of a large proportion of the species now can be worked out for the first time. A control block of limestone weighing one hundred and eighty-six pounds yielded ten thousand excellent specimens of invertebrates, including Foraminifera, brachiopods, bryozoans, gastropods, and pelecypods. Only a very few of these fossils were exposed on the surface of the rock and none could have been completely cleaned of matrix by mechanical means. Whole new faunas of mid-Ordovician trilobites preserved in the same way have been worked out by Whittington and Evitt (1954) and others.

One of the greatest obstacles in the study of fossil vertebrate remains has been the tedious and difficult extraction of the bones from hard rock matrix. The principal substance of vertebrate bones, conodonts, and certain brachiopods, is calcium phosphate

which is nearly insoluble in acetic and formic acids. These acids can, therefore, be used to dissolve limestone from phosphatic fossils. Many delicate and complex structures have been cleaned perfectly of hard matrix by this means. Usually the matrix contains much insoluble material so that the chemical preparation must be supplemented by manual cleaning under a microscope.

SUMMARY

These illustrations, I believe, demonstrate that the limitations of the fossil record are not so much a matter of poor preservation or insufficient quantity but rather insufficient collecting and inefficient methods of preparing fossils. New discoveries of fossils and rapid improvements in techniques have greatly expanded the possibilities for a far more complete knowledge of past life than we now possess. The future prospects for paleontology are, indeed, very bright if an ample supply of dedicated and expert paleontologists can be trained and oriented toward systematic exploration of the fossil record.

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PROGRESS IN PALEOBOTANY, 1908–1958

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ABSTRACT—The last fifty years represent the most productive period in the history of paleobotany, as is evident from many external and internal signs of progress. Among these are the growing number of active paleobotanists, the acquisition and establishment of more paleobotanical collections, the ever increasing number of published papers, catalogues, and books, and the more and more effective application of fossil plant materials for stratigraphic purposes and dating. Refined techniques, discoveries of new and highly productive localities, representative of nearly all fossiliferous ages and of widely separated geographic areas, and the introduction of many new viewpoints and concepts have greatly expanded the horizon and depth of paleobotanical research.

Integration of the results of related fields has materially advanced our understanding of fossil plants, their structure, mode of life, distribution, and evolution. The greatest advances have so far been made in regard to our knowledge of pteridophytes (ferns and fern allies) and gymnosperms (cycads, ginkgos, conifers, etc.). Intensive study of structurally preserved fossil material (wood, pollen, epidermis) of flowering plants (angiosperms) in addition to impression material is likely to result in many important and highly significant correlations and interpretations, especially of Mesozoic and Tertiary strata. Experimental studies in the newly established discipline of paleobiochemistry promise to yield even more spectacular results in regard to such elusive problems as the origin of life, the appearance of photosynthesis, and the nature and sequence of appearance of other basic biological processes.

FIFTY years ago paleobotany was an under-nourished stepchild. Today we look upon our science as a fully grown youth, whose physique is beginning to fill out through contact with an ever growing circle of borderline sciences, such as geophysics, biochemistry, petrography, and others. Before assessing the possible benefits accruing from these contacts, let us first consider the solid core of knowledge traditionally regarded as the realm of paleobotany.

Progress in paleobotany during the past fifty years has indeed been tremendous. The number of active paleobotanists has grown from a handful of devotées to a large and articulate group of well trained specialists. The paleobotanical section of the Botanical Society of America, organized some twenty years ago, is the first professional organization of paleobotanists ever formed anywhere. At the VIIIth International Botanical Congress in Paris (1954) a new international organization of paleobotanists was established and affiliated with the International Association for Plant Taxonomy. Fifty years ago, paleobotany hardly appeared in the curricula of our best universities. Today it is taught throughout the world in an ever growing number of institutions and recognized as a legitimate field for graduate study. A large segment of the research output of paleobotanists still appears in many botanical and geological journals, but at least two scientific journals are now limited to our field, *The Paleobotanist* and *Palaeontographica* (Section B). The number of paleobotanical laboratories is also growing, resulting in two instances in separate institutes entirely devoted to paleobotany, the Birbal Sahni Institute in Lucknow, India and the Palynological Laboratories, Pennsylvania State University. National and state parks have been set aside to preserve famous localities where fossil plants have been found in great abundance, such as the Petrified Forest National Monument in Arizona, the Ginkgo Petrified Forest State Park in Washington, and others. New techniques have greatly facilitated and hastened study of many fossil plants, whether petrified or otherwise preserved. New and fertile localities have disclosed unexpected, and previously unknown groups of plants and thus greatly affected our concepts of classification of the plant kingdom. Special provisions for fossil plants are now available in the *International Code of Botanical Nomenclature* (1956) and are likely to be refined this year at the IXth International

Botanical Congress in Montreal (Mamay et al. 1958). Great sums of money from governmental and private sources have been made available for paleobotanical research and given impetus to investigations that otherwise would have remained dormant. The world and all its fossiliferous horizons have become paleobotanical collecting grounds. In short, paleobotany is no longer a purely academic subject, as its influence reaches out into applied fields of endeavor and its contributions have been widely incorporated in our general knowledge of plants.

The scientific study of fossil plants in America is roughly one hundred years old, coinciding approximately with the establishment of the great surveys and the grand period of early exploration. Thus in a sense we are celebrating more than the fiftieth anniversary of the founding of the Paleontological Society. Lesquereux' studies of Carboniferous plants of Ohio and Pennsylvania began to appear in the 1850's and Dawson's classic paper, *On Fossil Plants from the Devonian of Canada*, was published in 1859. Scientific study of fossil plants started in Europe only in the early 1800s. One of the classic works of that early period is Sternberg's *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt* (v. 1, 1820), now the official starting point of paleobotanical nomenclature. On the other hand, Dawson's discovery and reconstruction of the genus *Psilophyton* from the Lower Devonian of Gaspé remained unappreciated and ignored until 1917, when the famous Rhynie chert fossils were described by Kidston and Lang.

Beautifully preserved structural material such as found in the Rhynie Chert beds (middle Devonian), Aberdeenshire, Scotland in 1913 is of course the most desirable kind for study. The anatomical detail available in such material makes it possible to describe these fossil plants in greater detail than that known about many modern plants. Soon followed by other studies of equal interest, this group of early vascular plants, now called Psilophytales, placed a new light on all other known vascular plants, leading to new botanical concepts and interpretations as well as systems of classification. The genus *Rhynia* for example became the model used for the exposition of the telome theory by Zimmermann in his famous book on *Phylogenie der Pflanzen* (1930). This theory has since been widely applied in the interpretation of other fossil plants, including the complex structure of conifer cones. In addition, the classification of the old group of Pteridophyta comprising ferns and fern allies has been greatly changed and completely reworked. Devonian plants of many kinds have also been described from western Europe, Spitzbergen, Wyoming, and lately Arizona. As a result, the Psilophytales no longer appear to be the homogeneous group of primitive vascular plants from which all other groups could be derived, as was long thought. Rather they constitute a heterogeneous group, perhaps of derivative character, now that vascular plants have been reported from Cambrian strata (Høeg 1958, Leclercq 1956). Even the Silurian psilophyte *Yarravia* and the equally old lycopod *Baragwanathia*, both from Australia, would no longer be the oldest known vascular plants. This honor may now go to a lycopodiaceous plant of Middle Cambrian age, collected in eastern Siberia and described by A. N. Kryschtofowitch in 1953, named *Aldanophyton antiquissimum*. Similar to *Baragwanathia* and *Drepanophycus*, *Aldanophyton* is structurally more complex than are the psilophytes. As this type of lycopod persisted from Middle Cambrian to Middle Devonian, some 200 million years, and other vascular plants may have been present, the origin of vascular plants probably occurred long before the Siluro-Devonian types of psilophytes came into being.

Even more famous are the beautifully preserved plant remains found in coal balls. Long known from the British Coal Measures and intensively studied by British paleobotanists, their study in the United States did not begin until 1922, when J. H. Hoskins cut the first American coal ball in the laboratory of Professor Noé at the University of Chicago. According to Andrews (1951) over 150 species of fossil plants have so far been described from American coal balls. On the basis of a survey of existing collections, Stewart (1958) found that coal ball floras may to a limited extent prove to be valuable indices of geological time along

with spores and compression fossils. He also suspects that coal balls from eastern Kentucky, the oldest known in the country, "may show close correlation with coal measure plants of British Isles and Europe," as may coal balls from several other localities in southwestern Indiana, western Kentucky, and southern Illinois, while coal balls found near New Castle, Texas are of Permian age.

Special methods have made it possible to obtain spectacular results in the study of carbonized materials, especially those of Mesozoic age. Outstanding examples of this type of work are seen in the detailed and far-reaching studies on gymnosperms published by Florin and Harris. Florin carried out a systematic survey of the cuticular and epidermal structures of all classes of gymnosperms, living and fossil. On the basis of structural differences in the formation and final appearance of the stomatal apparatus of gymnosperm leaves Florin was able to classify correctly much uncertain cycadophyte foliage material, examine the basis of our classification of gymnosperms, and restore fossil Cycadaceae to a far more prominent place. His reconstruction of the oldest known (Triassic) cycad, *Bjuvia simplex*, from associated but anatomically comparable organs, the leaf *Taeniopteris* and the megasporophyll *Palaeocycas*, will always prove the success of this method.

As increased knowledge of the Psilophytales and other pteridophyte groups changed our ideas and understanding of the classification of these plants, the classification of gymnosperms was changed on the basis of Florin's and Harris' work. In fact, the greatest advances in paleobotany have been made in regard to pteridophytes and gymnosperms. In no other groups of the plant kingdom has fossil material played such an important role in recasting our classifications. For instance, the classification of algae has been completely reworked on the basis of modern material without any recourse to fossil algae and the classification of flowering plants is still entirely dependent on our knowledge of living plants.

A very large segment of the paleobotanical literature is systematic and floristic, giving descriptions of the fossil plants encountered, usually arranged according to organs represented. Outstanding examples are: Dorf's study of Devonian floras of Wyoming, Read's preliminary description of the New Albany Shale flora (basal Mississippian) of Kentucky and the later studies on this flora by Hoskins and Cross, Arnold's study of the Michigan coal basin, White's Flora of the Hermit Shale, Arizona, Daugherty's monograph on the Petrified Forest in Arizona, Bell's monograph on the Lower Cretaceous Floras of western Canada, Berry's extensive studies of late Mesozoic and Tertiary floras of the southeastern United States and many parts of Latin America, Elias' studies on Tertiary Prairie grasses and other herbs from the High Plains, the comprehensive studies of western American fossil floras by Chaney and his numerous students, summarized by Axelrod (1958), Hollick's Tertiary floras of Alaska, Barghoorn, Spakman, and Traverse's studies of the Brandon Lignite, Vermont, and Wieland's detailed investigations on the Cerro Cuadrado Petrified Forest in Patagonia and the Liassic flora of the Mixteca Alta in Mexico. Among those published by European paleobotanists are: Høeg's study of the Downtonian and Devonian flora of Spitzbergen, Halle's basic studies of the Paleozoic floras of eastern Asia, Corsin's superbly illustrated monographs of French Carboniferous plants, Harris' exemplary studies of the Rhaetic floras of eastern Greenland and of the Jurassic flora of the Yorkshire coast of England, Reid and Chandler's famous flora of the London Clay, Godwin's History of the British Flora, and many others. The most readable and scientifically inclusive summary of our knowledge of fossil floras and their distribution as known in 1930 is found in Seward's *Plant Life Through the Ages* (1931). More recently Kräusel has given us a more compact and somewhat popular treatment in his *Versunkene Floren* (1950). A challenging account is found in Camp's *The Forests of the Past and Present* (1956).

Palynology is a wholly new and very active branch of paleobotany that has come into being in the last several decades. In the beginning concerned mainly with pollen obtained from Pleistocene and post-Pleistocene deposits, other spores and pollen of much greater age were soon included, the

oldest dating from the Cambrian of eastern Siberia. Adopting the pioneering work of Potonié, Raistrick, and Zerndt in Europe to American materials, Schopf, Wilson, and Bentall (1944) produced the first Synopsis of Paleozoic Spores that has served as a sound basis for further studies in this country and elsewhere. Presently, Kremp is compiling a much needed *Catalogue of Fossil Spores and Pollen*. The rapid growth of palynology makes a task of this kind an absolute necessity, if we are to avoid complete chaos and the introduction of thousands of superfluous names.

The immense stratigraphic value of these plant microfossils has been repeatedly shown, notably by Kosanke (1950) in regard to Illinois coal beds and by van der Hammen in Colombia (1957), Kuyl, Muller, and Waterbolk (1955) in Western Venezuela, and Couper in Great Britain (1958). Norem (1956) has been able to trace changes in the Tertiary floras described by Chaney, Axelrod, and others in corresponding changes of the populations of spores and pollen found in Tertiary sediments. Through the courtesy of Miss Leopold of the Denver Center of the U.S.G.S. I am able to quote unpublished data relative to the famous Florissant flora of Colorado. The description of this flora was begun by Lesquereux (1883), and continued by Kirchner, Knowlton, Cockerell, and others. In his excellent revision of this flora, MacGinitie (1953) had to dispose of 258 species of megafossils reported so far from this locality, of which "only about one half are valid." MacGinitie reduced these numerous entities to 114 species, representing 87 genera and 47 families, plus 30 forms of uncertain affinity, or 20 per cent of the total 144 forms. Study of microfossils of the Florissant formation yielded the following interesting results: 85 per cent of Coniferae substantiated by pollen, only *Torreya* being absent; monocotyledons corroborated 100 per cent by families, and among Amentiferae eight of the ten genera listed by MacGinitie represented by pollen, *Castanea* and *Populus* being absent. The other 29 families of dicotyledons are poorly represented by pollen, only six having been identified so far. As the wind-pollinated forms represent 90 per cent of the grain tallys in the pollen diagram, the unknown fraction is made up of numerically rare types. Pollen study has added 4 families and 7 genera of dicotyledons, and five members of lower groups of plants, or a total of 12 new genera. "The Florissant pollen flora shows a striking agreement within the wind-pollinated plant groups with megafossil determinations made by MacGinitie." Only two items were new on the basis of pollen records: *Fagopsis* should be placed in Fagaceae, not in Betulaceae, and *Juglans* is definitely a member of this flora. The poor representation of dicotyledonous families except those belonging to the Amentiferae may be due to the fact that they are predominantly insect-pollinated. As a result the identifiable portion of the Florissant flora has been increased from 87 to 99 genera, and MacGinitie's interpretation of the nature of this flora and its affinities has been fully substantiated.

Another famous locality is represented by the Mazon Creek area in Illinois. Fossils from it were first described by Lesquereux and subsequently by others. Although the number of reported species from this area and horizon is claimed to be about 500, perhaps less than half of them, possibly only about 100, are valid species. Unfortunately, no monograph of the flora of this region has ever been published. Neither do we have a monograph or series of monographs of American Carboniferous plants, including microfossils. Nor do we have adequate systematic monographs of many plant groups and individual genera (Just 1953).

The discovery during World War II of fossil *Metasequoia* in eastern Asia and the subsequent discovery of living trees in southcentral China have fired the imagination of paleobotanists, taxonomists, horticulturists, and journalists. It became the celebrated plant of the post-war period and thus was no doubt saved from complete extinction. Normally, living plants are found first and our generic concepts are based on them, and only later do we attempt to match fossil material with them. The story of the discovery of *Metasequoia* is simple compared with the seemingly endless series of errors committed by many paleobotanists in misidentifying fossil material referable to *Metasequoia*, *Sequoia*, and *Taxodium*, as detailed by Chaney in his *Revision of Fossil*

Sequoia and Taxodium in Western North America Based on the Recent Discovery of Metasequoia (1951).

Progress in paleobotany is regularly recorded, as follows: the American *Paleobotanical Reports* issued since 1929 under the auspices of the National Research Council, the last of which covering the period 1952–1957 has just been completed and will be published soon (Just 1959), *Pollen and Spore Circular*, now continued in *Micropaleontology*, *World Report on Palaeobotany* (1950–1956), *Reports of the Committee of British Paleobotanists*, Selling's two comprehensive reports entitled *Report on European Paleobotany*, the annual reviews of paleobotany published in *Fortschritte der Botanik*, Boureau and Depape's *Revue de paléobotanique, Palynologie* (Paris Museum), and Sahni's *Paleobotany in India*. Other immensely useful sources are Andrew's *Index of Generic Names of Fossil Plants, 1820–1950*, Knowlton's *Catalogue of Mesozoic and Cenozoic Plants of North America* and LaMotte's *Supplement* to it, LaMotte's *Catalogue of the Cenozoic Plants of North America through 1950*, Kremp's *Catalogue of Fossil Spores and Pollen*, and the published parts of Jongmans' *Fossilium Catalogus, Plantae*.

Paleobotanists have two methods at their disposal for expressing the present status of knowledge about fossil plants and their purported relationships with living ones. The first method is systematic using a revised system of classification. For example, Moore (1954) advocated dividing the plant kingdom into two and adopting Haeckel's classic term Protista (1866) for one of these kingdoms. Lam, on the other hand, attempted to align the vascular plants in evolutionary sequence conforming roughly to the existing divisions of geological time, and designated the major groups accordingly as *Palaeostelocormophyta*, *Mesostelocormophyta*, and *Neostelocormophyta*.

The other method involves the use of reconstructions, executed as drawings, paintings, or three-dimensional models. Bertrand and Corsin (1950) published a suite of such paintings prepared under their direction. Kräusel (1949) traced all those pertaining to carboniferous forests and Jongmans (1949) brought together all known and paleobotanically important illustrations. Models of fossil plants have been made in various institutions, particularly in Chicago Natural History Museum. I have always referred to work of this kind as three-dimensional morphology, a distinct contribution made by museums.

On the eve of the centenary of the publication of that great classic of biological literature, *The Origin of Species by Means of Natural Selection* by Charles Darwin, it seems more than appropriate to comment on the place of fossil plants in regard to our present knowledge of evolution. H. Hamshaw Thomas (1958) has just given us such an appraisal from his point of view under the title *Fossil Plants and Evolution*, published by the Linnean Society of London as one of thirteen contributions to its *Darwin-Wallace Centenary*. According to Thomas, "the geological record of plant life on the earth as known to Darwin and Wallace provided no support to the theory of Evolution." Thomas also quotes the Nestor of British paleobotanists, D. H. Scott, who in assessing contemporary knowledge of fossil plants in 1909 was of the opinion, "that the records of plant history suggested a connection between some of the main groups of living forms, but that they provided little evidence of the derivation of one species or genus from another." And Thomas himself states in the conclusions reached by him, "Owing to the comparative rarity of conditions favouring the preservation of plants as fossils, no long series of forms have been found from which the evolutionary history of species or genera can be determined." Actually, several interesting examples of speciation have been recorded in the paleobotanical literature.

The pteridosperm species *Stenopteris elongata*, as found in the Ipswich Coal Measures (Middle Triassic) of Queensland, Australia, occurs in all known horizons ranging throughout 4,000 feet thickness of this formation. Considering the time factor involved for the deposition of this formation, Jones and de Jersey (1947) concluded that the specimens examined by them belonged to an evolutionary series with a marked trend toward increased complexity of frond type. 1) Pinnate fronds, the simplest ones, are found near the base of the series. 2) Bipinnate fronds appear next, the lobes being

either without or with veins, designated by them as *S. spinifolia.* 3) Specimens from even higher horizons show two or three lobes in ultimate pinnules; this form is now called *S. tripinnata.* Interestingly enough the simpler forms do not disappear at the time when succeeding types have been developed, rather they decrease markedly in abundance.

A fine example was worked out by Roland Brown with reference to the modern Katsura tree, *Cercidiphyllum japonicum.* In his exemplary revision of this genus Brown (1939) recognizes five form species based on a total of more than 125 previously described fossil plants variously referred to the genera *Populus, Grewia, Leguminosites,* etc. "These five norms indicate an evolution of leaf form from elliptic in the Cretaceous to strongly cordate in the living species. The latter, like *Ginkgo biloba,* may, under some conditions, reproduce all the forms represented by the fossil leaf norms."

Finally, the concept of ecospecies employed in modern experimental taxonomic and genetical research, has been applied to various Tertiary fossil plants by Axelrod (1941) and Mason (1942), specifically to fossil equivalents of modern endemic trees and shrubs which occupied habitats widely differing from those of their nearest descendants. Apparently our modern endemics survived in habitats different from those once occupied by their related fossil forms as a result of the elimination of biotypes during late Cenozoic.

The leaf changes here recorded can be regarded as illustrations of what Zimmermann called *Merkmalsphylogenie,* or in Mrs. Arber's words, *phylogeny of single characters* as opposed to the phylogeny of major groups involving large complexes of characters. Fossil plants give ample evidence of these processes (Stebbins 1950). This category includes such time-honored and unresolved problems as the origin of flowering plants, origin of algae, origin of fungi, etc. In regard to the origin and classification of marine algae, Miss Tilden's ingenious theory, expounded first in 1933 and later in her book (1935), has not yet received the attention it deserves. Her color plate shows the hypothetical origin of the various algal groups as projected into the distant geological past. She recognizes five algal periods, beginning in the Archaeozoic era with the cyanophycean period (marine) and ending with the chlorophycean period (freshwater) at the end of the Proterozoic. As all major algal groups are characterized by distinctive photosynthetic pigments and metabolic by-products, the pigments characteristic of each algal period are shown in color. Comparative biochemistry will have to find the answer in regard to the sequence of appearance of the various pigments unless their derivatives can be found in sediments, as shown for chlorophyll by Orr et al. (1958).

Thus we have arrived at that great pre-Cambrian vacuum that until recently was being filled only with highly questionable fossils and a multitude of often more questionable theories. [We could call the Azoic and Proterozoic by a joint name, the Agnostozoic. This would not advance our meager knowledge greatly.] In his critical evaluation of pre-Cambrian fossils Schindewolf (1956) admits the possibility of the presence of great masses of unicellular algae and perhaps somewhat more advanced forms in pre-Cambrian oceans. The discovery by Tyler and Barghoorn (1954) of organisms of simple organization in rocks of Lower Middle Huronian age, preserved in dense, non-ferruginous cherts of the basal members of the Gunflint iron formation along the north shore of Lake Superior in Ontario, Canada, has provided us with the oldest real fossils known. "These plants, as they may best be called on the basis of morphology, are primarily filamentous structures organized in colonies varying from actinomorphic aggregates to random groups of unbranched, septate filaments" (Barghoorn 1957). Another remarkable fact is that by rigorous analysis eight amino acids were determined chromatographically in the Gunflint chert (alanine, proline, glycine, glutamic acid, valine, leucine or isoleucine, aspartic acid, and lysine).

This brings us directly into the realm of the new science of paleobiochemistry. Abelson, who studied the Gunflint chert claims (1957) that "Organic chemicals of biological origin are being found in an increasing number of fossils, sediments, and sedimentary rocks." Through exploration of such material we may come a great deal closer to

what seemed to be a wholly philosophical problem, the Origin of Life. Although Seward in his famous book says that "Geology tells us nothing of the origin of life," we can now hopefully look toward the day when it will. A symposium held at the New York Academy of Sciences in 1957 was devoted to *Modern Ideas on Spontaneous Generation*. At this meeting 19 participants presented 13 papers dealing with various aspects of this important event. They discussed not only the findings of paleobiochemistry but also presented evidence of experiments designed to simulate conditions on this planet that may have preceded life and led to spontaneous generation. When, where, and how these eobionts or probionts appeared, remains uncertain. But we have at least found an experimental basis for attacking special phases and aspects of this complex problem and we may look to the science of paleobiochemistry to enlighten us about organic materials preserved on this planet that may aid in deciphering the long and arduous road taken by all forms of life since the time that it emerged "from a nonliving milieu" (Blum 1957).

Our goal for the future was well formulated by Thomas in his address at the Darwin-Wallace Centenary. He advocated that the investigation of fossil plants should embrace all aspects of study "with the object of discovering how plants have come to be organisms such as we now see them."

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FIFTY YEARS OF MICROPALEONTOLOGY

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THE term Micropaleontology has come into common use only in the past half century. It will be found in few dictionaries and a definition satisfactory to everyone is probably impossible to formulate. Daniel J. Jones (1956) in his "Introduction to Microfossils," gives the following definition: "A microfossil is any fossil (usually small) whose distinguishing characteristics are best studied by means of the microscope." He would include the study of fossils in thin sections, and thus would include by that means the remains of the entire animal and plant kingdoms. This is a development of the ideas expressed in the excellent article by Carey Croneis (1941): "Micropaleontology —Past and Future," to which one may well turn for historical details in the development of this field of study.

Micropaleontology to the oil industry, however, has from the first meant essentially a study of foraminifera, ostracoda and other organisms which are small enough to be obtained without crushing from well cores. Obviously it would be impossible to discuss all microfossils under Jones' definition. I will therefore confine this discussion essentially to the developments which have taken place in the study of foraminifera and ostracoda, with only minor mention of the other groups, many of which are being covered by other speakers on the program.

FORAMINIFERA

In the period under discussion Foraminifera have been the most useful of all fossils. Their extraordinary abundance in marine sediments, a cubic inch of core frequently containing several thousand well preserved specimens, and their convenient size permitting their study with wide-field binocular microscopes, has made them extremely easy to use and to file for future reference. Moreover, the paleontologist has had the great advantage in this group of fossils that the classification, however artificial, has been based on the hard parts, or "test," rather than on parts which are not preserved in fossilization.

Those interested in the history of foraminiferal study prior to this century will find a satisfactory discussion in Chapman's (1902) textbook: "The Foraminifera."

During the early years of this century, most geologists had little interest in foraminifera, other than as objects of beauty. It was assumed that foraminifera, being single-celled organisms, were long ranging, and that most types had already been well illustrated and described. This attitude is clearly illustrated by Rufus Mather Bagg's (1912) paper on the "Pliocene and Pleistocene Foraminifera from southern California." It was beautifully illustrated with 28 plates copied from Brady's *Challenger Report*, or from Flint, Goes, Jones and other earlier authors, rather than from the specimens which he had examined from California. When the Pleistocene portion of this fauna was critically restudied by Galloway & Wissler (1927), 79 species were encountered, 41 of which were new, and of the previously described species, none were left under the names Bagg had indicated.

As far as I know, the first micropaleontologic work done on well samples in this country was that of Hilgard & Hopkins (1878, 1884). The work was actually done by Hopkins under Hilgard's direction. The first paper was a well illustrated report on the microscopic fossils encountered in a well at New Orleans; the second on borings across the Mississippi Valley between Memphis and Vicksburg. Both contributed greatly to our knowledge of Gulf Coast stratigraphy, but as both were published in the U. S. Engineers reports of the War Department, they have been overlooked by micropaleontologists to this day. Similar studies were made by Udden (1914) in Illinois and by Cushman (1914, 1919) in South Carolina and Florida.

Credit for the revolution which took place in the use of foraminifera properly goes to the three ladies Esther Richards Applin, Alva E. Ellisor, and Hedwig T. Kniker. Their paper on the "Subsurface stratigraphy of the coastal plain of Texas

and Louisiana" (1925) had been presented before the Annual Meeting of the American Association of Petroleum Geologists in Shreveport, and the discussion which followed opened the eyes of oil company executives. Thus an immediate demand arose for micropaleontologists and courses were instituted in many universities. By 1941 Croneis estimated that over 500 micropaleontologists were employed by the petroleum industry.

The rush to describe the fossil microfaunas of the world gained steady momentum, and in the race to describe the fossil foraminifera Dr. J. A. Cushman had a long head start. He was the recognized authority with at least 50 papers to his credit and had organized the Cushman Laboratory for Foraminiferal Research at Sharon, Massachusetts. To this Laboratory came students from many parts of the world. Others sent him faunas to describe, and the Memorial Volume, issued after his death in 1949, lists a total of 557 titles, most of which dealt with foraminifera.

The Society of Economic Paleontologists and Mineralogists had its inception in March, 1926, and was formally organized a year later. The first issue of the *Journal of Paleontology* appeared in July 1927. In 1935, the Paleontological Society joined in the publication of the Journal with the issuing of volume 9 and since that time has been responsible for more than half of the pages printed. Many other excellent journals, such as *Micropaleontology*, have appeared; the latest being the *Journal of the Paleontological Society of India*. With a rising number of micropaleontologists there has been a steadily increasing volume of publication.

How many valid species of foraminifera have been described no one could tell at present. As a means of helping the systematists in this field, Dr. Brooks F. Ellis and Angelina Messina of New York University, in cooperation with the American Museum of Natural History and W.P.A., compiled the *Catalogue of Foraminifera*, which at the present time amounts to 46 volumes, 45 of which contain pictures and descriptions of genera and species. Each volume holds about 700 sheets. Some species require more than one sheet, and allowing for generic and subgeneric sheets, it would appear that the Catalogue records well over 20,000 species. This does not mean that there are that many valid species, however. This is well illustrated by Boltovskoy's (1958) recent experience. When studying *Nonion affine* (Reuss, 1851) in the National Museum, he found the species catalogued on 18 different slides, under 10 different names, six of which were described as "new." The same species is probably to be found under different names in other museums. There can be no doubt that foraminiferal literature is overloaded with both homonyms and synonyms, and accurate specific identification is very difficult.

Generic classification is, however, becoming even more difficult. Many attempts were made in the nineteenth century to work out a classification of this Order. Chapman, with only a few modifications, adopted the classification of H. B. Brady (1884) as given in his *Challenger Expedition Report.* This classification was simple, consisting of but 10 families and 28 subfamilies, and was based on chamber arrangement and on the composition of the test. Cushman used it in the first 50 or more of his reports. However, when he started teaching foraminifera at his Laboratory, Cushman (1927) published "An Outline of a Re-classification of the Foraminifera." In this classification he used 45 families, with little use of subfamilies. This reclassification was expanded the next year into a textbook: *Foraminifera, Their Classification and Economic Use*, which went through a number of expanded editions. In the last edition of 1950, Cushman classified foraminifera under 50 families. During this period of a little more than 20 years it was generally accepted and used by a majority of foraminiferal workers throughout the world, particularly by those engaged in oil company work. This general acceptance was fortunate, as it provided a period of relative stability in taxonomy while thousands of useful species were being described, and it made possible the writing of company reports which could be understood by persons not trained in micropaleontology.

Cushman's classification was not universally adopted, however. Galloway (1933) published his *Manual of Foraminifera*, showing a number of early genera which Cushman had not included and his arrangement in a

number of cases was different from that of Cushman.

Chapman & Parr (1936), in the Proceedings of the Royal Society of Victoria, recognized the merits of much of Cushman's work, and then proceeded to re-arrange Chapmans' previous classification, ending up with 3 super-families, 33 families and 86 sub-families. Because of its place of publication, this did not attract wide circulation or acceptance. It was however, an opening wedge. Glaessner's (1945) *Principles of Micropaleontology* gave a quite different classification and approach to foraminifera from that of Cushman. This was followed by Hofker (1951) with many revisions and by Bermudez (1952) who revised the rotaliform foraminifera, and by many other papers which together have essentially extinguished the Cushman system.

To gain a partial idea of what has happened to foraminifera since Cushman's death, I have consulted the Annual Bibliography and Index of Foraminifera published by Hans Thalmann in the *Journal of Paleontology* for the years 1949 to 1955, the latter year having been published this past July, in what Thalmann states is an incomplete manner. This incomplete record for 7 years shows a total of 3,261 papers on foraminifera had been published in which were erected:

1	Order
7	Suborders
2	Superfamilies
46	Families and subfamilies
303	Genera and subgenera
4,083	New species, varieties and names
4,441	New names or nearly 2 new names per day for a period of 7 years.

The reason for the increasing delay in the appearance of Thalmann's Bibliography and Index has been his desire to include the rapidly increasing volume of rather inaccessible Russian literature. It was omitted entirely from the 1955 list, just published. It may well be that the Russians, in their expanding program to describe the fossil foraminiferal faunas of their vast territory are creating the same problem in foraminiferal taxonomy that I will discuss later for the case of ostracoda. It is certain that they have produced an abundant literature. Thalmann's 1954 Bibliography and Index gives the names of 34 Russian authors who had described foraminifera, but he had seen the papers of only half of them. As further illustration I examined volume 8 of the *Microfauna of the USSR* (1955), which contains 4 foraminiferal papers in which are described 3 subfamilies and 13 genera. Of these 11 were given as new and 5 carried dates back as far as 1948, but had not been encountered by Thalmann. Submitting a list of these terms to several professors of micropaleontology, I found as might be expected that they had never heard of any of them.

Even without the Russians and their contribution to the complexities, it is obviously impossible for professors of paleontology to obtain and read over 3,000 new articles on their subject in so short a time. They, therefore, cannot keep up with the taxonomic changes, though many of them attempt to do so in an endeavor to give their students the latest names for the objects being studied in class. A doubling of major classificatory terms in a 7-year period without any text-book to show such changes is obviously an impossible situation from a teaching standpoint. The result is likely to cause the class confusion as students have difficulty in understanding why so many of these terms do not appear in their textbook, regardless of which book is used. The effect apparently has been for some time to cause a reluctance on the part of students to enter the field of micropaleontology. Oil companies for some years have been having difficulty in finding satisfactory new micropaleontologists.

The effect on oil company micropaleontologic activities is likewise not pleasant. Quite obviously it is impossible for any company to keep each of its district laboratories equipped with all of these publications, and even if they did, the paleontologists would have to spend all of their time reading and digesting the literature, instead of making identifications of samples. Moreover, annual changes in generic names for species in company reports would mean that company executives would have to be foraminiferal experts to understand them. Many surface and subsurface zones are named for genera in use a score of years ago, and these stratigraphic terms cannot be changed at

the whim of some taxonomist. In the opinion of the oil company paleontologists, with whom I have discussed this problem, the taxonomic situation is best described under the single word "Chaos."

It was a realization some years ago that this chaotic condition was approaching in foraminifera that caused me to switch my major attention to ostracoda and leave the teaching of foraminifera to others. In the discussion which follows it will become apparent that ostracoda likewise may soon approach a similar condition.

OSTRACODA

The year 1958 marks the 200th anniversary of ostracod taxonomy. Linnaeus (1758) used the generic name *Monoculus* for 9 species of arthropoda, at least one of which has been considered to be an ostracod. though currently thought to be an unidentifiable one. Real systematic work on ostracoda dates from the papers by O. F. Muller (1776, 1785) in which the genus *Cypris* was erected for fresh-water ostracoda and *Cythere* for marine forms.

Further subdivision of the ostracoda was very slow. Families were created by Baird (1845, 1850) and by Dana (1853), but the major classification of living ostracoda was worked out by G. O. Sars (1866), as a young man, and which he expanded slightly in his later years (1922–1928). This classification was zoological, based on the appendages, which are not preserved in fossilization. Its major features have been accepted, however, by all workers for post-Paleozoic and recent ostracoda.

The classification of Paleozoic ostracoda has had quite a different history. My records show a total of 101 superfamilies, families and subfamilies have been erected for Paleozoic ostracoda to the middle of 1958. Of these, the first, *Leperditidae*, was erected by Jones in 1856. To the end of 1907 only 13 terms had been created. But since 1947, 52 terms have been created, or more than half of the total, of which 17 are of Russian origin.

From the beginning it was recognized that many of the Paleozoic ostracoda had no living representatives. This culminated in a classification worked out by Ulrich & Bassler (1923) which was based almost entirely on external characters, and which resulted in reversing the normal orientation for many forms, the posterior being given as the anterior, and the left valve being taken for the right. It was not until Triebel (1941), in his paper on the morphology and ecology of fossil ostracoda, demonstrated beyond any question the proper principles for orientation of these forms that many Paleozoic workers accepted a different orientation.

Confusion in Paleozoic ostracod taxonomy, therefore, bears some resemblance to that existing in the foraminifera. If one examines the "Handbook of Ostracod Taxonomy," Howe (1954), he will often find that a single genus has by succeeding authors been placed in as many as 6 or 7 different families.

Ostracoda have thus been studied by three separate groups of workers, the zoologists working with recent forms, the students of Paleozoic ostracoda, and a smaller group working with post-Paleozoic ostracoda. Only the latter group has paid much attention to what the other groups were doing. They have been handicapped because the zoologists did not properly described the carapace, and likewise handicapped because the Paleozoic workers usually did not describe any of the internal details of the carapace, and because the described forms were oriented in a manner quite unfamiliar to them, and the terminology was almost entirely unlike that of the zoologists.

Fortunately there have been compensating factors. Bassler & Kellett (1934) published a voluminous *Bibliography and Index of the Paleozoic Ostracoda* in which the Ulrich & Bassler classification was expanded and illustrated. More recently Wagner (1957) has illustrated beautifully the carapaces of many of the type species of recent ostracoda of northwestern Europe. It appears now that with proper use of the finer features of the ostracod carapace such as hinges, muscle scars, marginal areas and the characters of the various normal, radial and pseudoradial canals that a natural classification of ostracoda may become possible if the taxonomy does not become too complex to be workable before such a classification is derived.

With the hope of stabilizing ostracod nomenclature so that the ostracod volume

of the Treatise on Paleontology could be prepared, I published in (1954) a "Handbook of Ostracod Taxonomy." From this it may be found that 274 familial and generic names had been created in the first 150 years of ostracod study. Thus in 1907, of the 274 taxonomic terms, 175 had been created by zoologists, and 99 by paleontologists. Of the names created by paleontologists, 88 were for Paleozoic ostracoda and only 11 for post-Paleozoic ostracoda. All told some 1098 taxonomic terms were given in the Handbook, but many of these were invalid for various reasons.

The desired stability has not been achieved. Instead, I have a record of 355 names which have been proposed in the $3\frac{1}{2}$ years since publication of the Handbook. Of these 183, or more than half, have been proposed by Russian paleontologists. In addition over 200 genera have had their family assignments changed. It appears certain that I do not have as much as half of the current Russian literature, but what I do have is enough to show that since the publication of Schweyer's (1949) series of articles on the morphology and classification of fossil ostracoda a whole new Russian literature has developed. In this they have not confined themselves to Russian species, but have selected as types for their new genera many species by western authors such as T. R. Jones, Williamson, Roemer, Lienenklaus, G. W. Muller, Hornibrook and myself.

These Russian publications since 1948 are not to be ignored. Unlike earlier publications, they are printed on good paper, many of the books are cloth bound, and most of them are beautifully illustrated. Not all of the names used are acceptible under the rules of nomenclature. Some are homonyms, some synonyms, and some are based on a misunderstanding of earlier work by non-Russians. A number of the new genera are published in more than one publication under different dates. However, the ratio of invalid to valid terms appears to be no greater than occurred in the first 150 years of ostracod study. The most important feature is that these Russian reports show their authors are familiar with the finer details of the carapace, and the new taxonomic units are not based on external characters alone.

OTHER MICRO-ORGANISMS

Summary taxonomic studies have been published recently by Bassler (1953) for fossil Bryozoa, by Campbell & Moore (1954) for Radiolaria and Heliozoa, and by Collinson & Schwalb (1955) for North American Paleozoic Chitinozoa. Frizzell & Exline (1955) have put together existing information on fossil Holothurian sclerites. Difficulties in conodont classification have been clearly brought out by Rhodes (1952). Smiser (1933) demonstrated that echinoid fragments could be used in upper Cretaceous correlation. A classification of fragmentary crinoidal remains was attempted by Moore (1939). Howe (1942) in a paper on "Neglected Gulf Coast Tertiary Microfossils" pointed out the utility of such other microfossils as ophiurans, comatulids, starfish plates and barnacles. However, none of these fields of inquiry have attracted many workers, and fossil otoliths, which are used extensively in Europe, have remained entirely neglected.

CONCLUSIONS

Perhaps the increasing complexities of foraminiferal and ostracod nomenclature, and the almost insurmountable problems of keeping up with the steadily increasing literature in both fields will cause future micropaleontologists in self defense to take up some of the promising fields which are now largely neglected.

The soundest conclusion to be drawn from the figures which I have presented is that, in the absence of a central translating agency, American micropaleontologists must learn Russian and learn it quickly. In the field of foraminifera Russian has obviously become the most important foreign language. In the field of ostracoda, it is clearly more important at the present time than all other foreign languages combined.

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SYMPOSIUM PAPERS

Three papers in this number are parts of a symposium on Fifty Years of American Paleontology, presented at the Jubilee Meeting of the Paleontological Society, St. Louis, Missouri, November 8, 1958. The other three papers will appear in later issues.

ERWIN C. STUMM, *editor*

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